

## Linkage Map of *Salmonella typhimurium*, Edition V

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### INTRODUCTION

We present the fifth edition of the linkage map of *Salmonella typhimurium*, comprising 423 genes. The original 1965 compilation in this series included 133 gene loci (531); the loci included in succeeding revisions were: 1967, 188 (526); 1970, 251 (527); and 1972, 323 (529). Where possible we have eliminated references to the earlier literature, and the reader is referred to the prior reviews. In addition, we have had to skip accessory references which we decided were not central to the themes selected for coverage. We present a synopsis of where *Salmonella* genetics stands today, with a focus on the genetic architecture of the *Salmonella* chromosome. We summarize advances that promise to increase interest in *S. typhimurium* as a system for genetic investigation, as well as to increase its use as an investigatory tool in other areas of biology. Genetic techniques and progress in biochemistry and comparative bacteriology/virology are interwoven with elucidation of gene structure/function relationships. To maximize the usefulness of this review, we have included brief descriptions of newer aspects of genetic manipulation and some references to papers concerned with enzymology and enzyme regulation in *S. typhimurium*. References to pertinent phages and plasmids, as well as to certain critical loci in other *Salmonella* spp. and *Escherichia coli*, are included. This latter extrapolation appears warranted since it is clear that the genetic maps of *Salmonelleae* and of *E. coli* bear a great degree of homology in overall genetic organization (55,

426, 528, 530) as well as in deoxyribonucleic acid (DNA) sequence homology determined by in vitro DNA-DNA hybridization techniques (96, 148).

### THE LINKAGE MAP

We have made three modifications in the linkage map for the convenience of workers in the field and in recognition of homologies known to exist between *S. typhimurium* and *E. coli*. First, we have normally utilized mapping data for *S. typhimurium* but, where *Salmonella* data are scarce, we have extrapolated positions of several key loci from the newly determined 100-min time-of-entry map of *E. coli* (46). Thus, our map also constitutes 100 units (U) whereas the time-of-entry data indicate 138 min of entry time in Hfr crosses (529). The reasons for the change are: (i) since most genes are presently mapped only approximately by conjugation, and then located more precisely by transduction, the "minute" as a measure of map location becomes correspondingly less important; (ii) the difference in time-of-entry studies between *S. typhimurium* (138 min) and *E. coli* K-12 (100 min) is probably due to differences in the rate of transfer of the chromosome by different Hfr strains rather than a difference in physical length; and (iii) the continued observations of genetic homology between *S. typhimurium* and *E. coli* make the use of a similar metric very valuable. Figure 1 shows a number of reference genes on the linkage map in its familiar circular form.

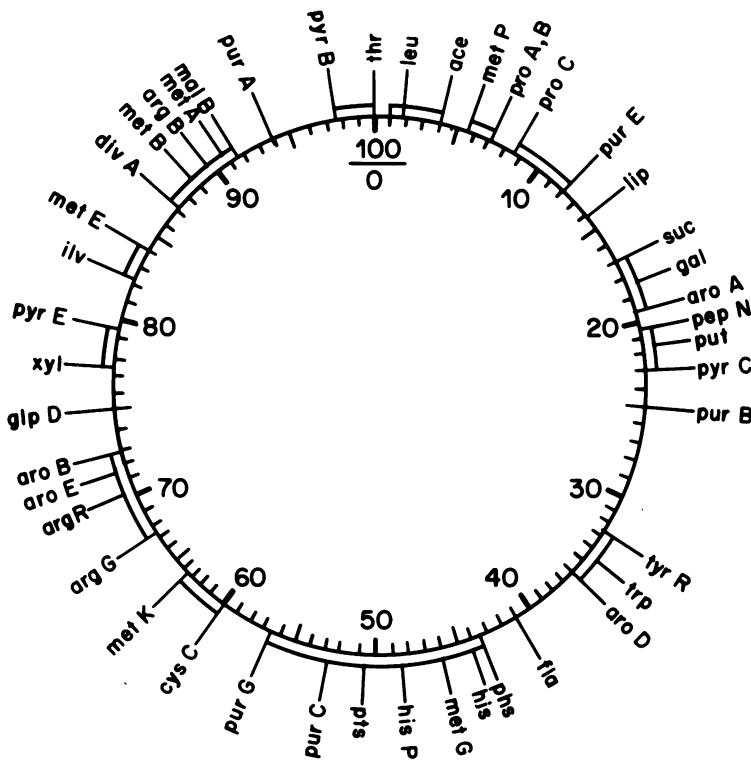


FIG. 1. Circular linkage map of *S. typhimurium* drawn to 100 units (U) rather than the length of 138 min previously presented in reference 529. Consult text for an explanation of the change. The interval length between some reference markers is taken from the linkage map of *E. coli* K-12 (46), but most intervals have been determined directly in *S. typhimurium*. Double lines indicate blocks of genes that comprise continuous linkage groups, based on transduction with phages P22, KB1, ES18, and P1. A single line indicates regions for which transduction linkage groups covering two or more unit lengths have not been detected. For an explanation of the symbols, see Table 1; a detailed linkage map is presented in Fig. 2.

Blocks of genes which comprise continuous transduction linkage groups are indicated by double lines; the most frequent transducing phage used has been P22, but ES18, KB1, and P1 have also been studied. In other regions, shown with a single line, some transduction between genes may have been observed (this can be determined in Fig. 2), but linkage groups covering 2 U or more have not been detected.

Second, for convenience, we have presented the complete map in 10 linear 10-min intervals in Fig. 2, where all the genes are illustrated, rather than in the circular form. Since our 100 U do not abide by the *Salmonella* time-of-entry data of 138 min (529), we have chosen to base the units on P22 "phage lengths." P22 can encapsulate  $26 \times 10^6$  to  $27 \times 10^6$  daltons of DNA (494, 547); this is about 1/100 of the total *Salmonella* chromosome (392). The linear distance between genes is calculated from the P22 cotransduction data by the formula derived by Kemper (323),  $c = 1 - t + (t \times \ln t)$ , where  $c$  = cotransduction frequency, and  $t$  = linear dis-

tance between genes, measured as the fraction of the length of the DNA of a transducing particle. A similar model was used previously (46); as for *E. coli*, we assigned a 2-U length to the P1 transducing fragment, while those of P22, KB1, and ES18 were each assigned a 1-U length. In Fig. 2, parentheses around a gene symbol indicate that the location of a marker is known only approximately, usually from conjugation studies. An asterisk indicates that the gene has been mapped more precisely, usually by transduction, but that its order with respect to adjacent genes is not known. Especially for genes shown with parentheses or asterisks, the reader is not only encouraged, but in fact is warned, to consult original references with regard to detailed linkage data; our compilation is intended to lead to the original literature, not replace it. To indicate the source of the data used to determine the transduction linkage groups, the linear distance between genes, determined from cotransduction data, and the reference from which the data were taken are shown in selected cases (Fig. 2).

The third step we have taken is to standardize more closely genetic nomenclature with that for *E. coli* (46), maintaining the original format and purpose of the system of Demerec et al. (159). Present symbols are found on the updated linkage map (Fig. 2) and in the descriptive table (Table 1), and, as a supplement to Table 2 of Bachmann et al. (46), we include a table of outmoded designations (Table 2). Elsewhere suggestions are given pertaining to symbols for mutations leading to temperature sensitivity (255) or defects in protein synthesis (120). Not everyone will be happy with the symbols we have decided to adopt; particular choices will decrease the ease with which past literature can be followed, and some choices fail to retain priority of first usage. The intent is to help the researcher and to minimize changes in the future. We feel that a change in a symbol does not violate the basic aspects of scientific discovery and that confusion in the years ahead will be lessened if homologous loci receive homologous titles in closely related bacterial species. The clearinghouses for gene symbols and allele numbers will attempt to continue coordination as they have in the past: *Salmonella* users should consult Kenneth E. Sanderson, and *E. coli* users should consult Barbara J. Bachmann (Yale University School of Medicine, New Haven, CT 06510).

We encourage careful record keeping on the complete genotypes of strains isolated or imported into the laboratory; where possible, the revised nomenclature listed here and in the article by Bachmann et al. (46) should be used. In all cases, the recipient of a culture or the reader of a paper should be informed as to what the symbols imply.

Modern bacterial genetics utilizes an array of episomes, plasmids, and transposable elements. We suggest that workers using these elements follow the guidelines of established nomenclature (386) as recently extended (112, 113, 449).

The linkage maps of *E. coli* K-12 (46) and *S. typhimurium* (Fig. 2) show overall homology of gene location, which supported the decision to display the linkage map of *S. typhimurium* as 100 U. However, a few differences between the genera have been observed. The gene segment including *pyrF-cysB-trp* was found to be inverted (532), and the size of the inverted segment was shown to include up to 10% of the entire chromosome (117). A comparison of a segment of the maps of the two genera (Fig. 3) suggests that inversion of the portion 25.5 to 36.5 U has occurred. In *S. typhimurium*, the order of the genes from *tyrR* (33 U) to *aroD* (36 U) is determined by joint transduction studies (Fig. 2), and the orientation of this group is determined by

conjugation crosses (reviewed in reference 532). HfrB2 of *S. typhimurium* transfers *tre* (534) and *chIC* (115, 117) as proximal markers, but *ptsG*, *tdk*, *galU*, and *trp* are transferred as distal markers. In *E. coli* K-12, *tre* is counterclockwise from *trp*, linked to *purB* by P1 transduction (57). Another feature which confirms the existence of the inversion is the originally puzzling observation that the *his-trp* time-of-entry interval is very long (17 min) in *E. coli* (46) but much shorter (13 min) in *S. typhimurium* (531), although the total map of *S. typhimurium* (138 min) is longer than that of *E. coli* (100 min); the *his-trp* interval is shown as 10 U in Fig. 2. This suggests that the *trp* genes are near one end of the inverted segment and that the *trp*-containing end is attached close to the *his* side in *S. typhimurium* and on the side not containing *his* in *E. coli* (Fig. 3). Uncertainties about locations of a few genes make the exact inversion points still unclear. Conjugation crosses with SU418 (HfrB2) in *S. typhimurium* show *purB* to be distal, hence outside the inverted segment (K. E. Sanderson, unpublished data), but *ptsG* is located by Z. Hartman (unpublished data) in the *his-trp* interval. In *E. coli*, the order *pyrC-ptsG-purB* indicates that, if *ptsG* is inverted, *purB* should also be. In addition, although *aroD* in *S. typhimurium* is shown in Fig. 3 to be at 36 U, based on transduction studies, and outside the inverted segment, it appears to be a distal marker in HfrB2 and SA828. A second difference between the linkage maps is that *pyrB* is located at 98 U in *S. typhimurium*, in a transduction linkage group with *deo-serB-thr*, while in *E. coli* *pyrB* is at 95 U, 5 U from *thr*, and separated from it by one of the two breaks in the transduction linkage map of *E. coli* (46); there seems to be an insertion of genetic material into the *E. coli* chromosome at this point, or in this segment, as in the *trp* region, the two genera may differ by an inversion.

There are also several cases in which a gene has been mapped for one genus, but the presence of the gene and its related function cannot be demonstrated in the other. Genes for lactose (*lac*) and tryptophan (*tna*) utilization have been mapped in *E. coli* but are absent from *S. typhimurium*. Genes for histidine utilization (*hut*) have been mapped in *S. typhimurium* but are absent from *E. coli*. The gene for phase-one flagellar antigen of *S. abony* (*H1*) is allelic to *hag*, the gene for the only flagellar antigen of *E. coli*, whereas the *S. abony* gene *H2* has no counterpart in *E. coli*. Comparisons of the linkage maps of all members of the *Enterobacteriaceae* on which data are available have been published (528, 530).

In certain cases, different alleles of the same

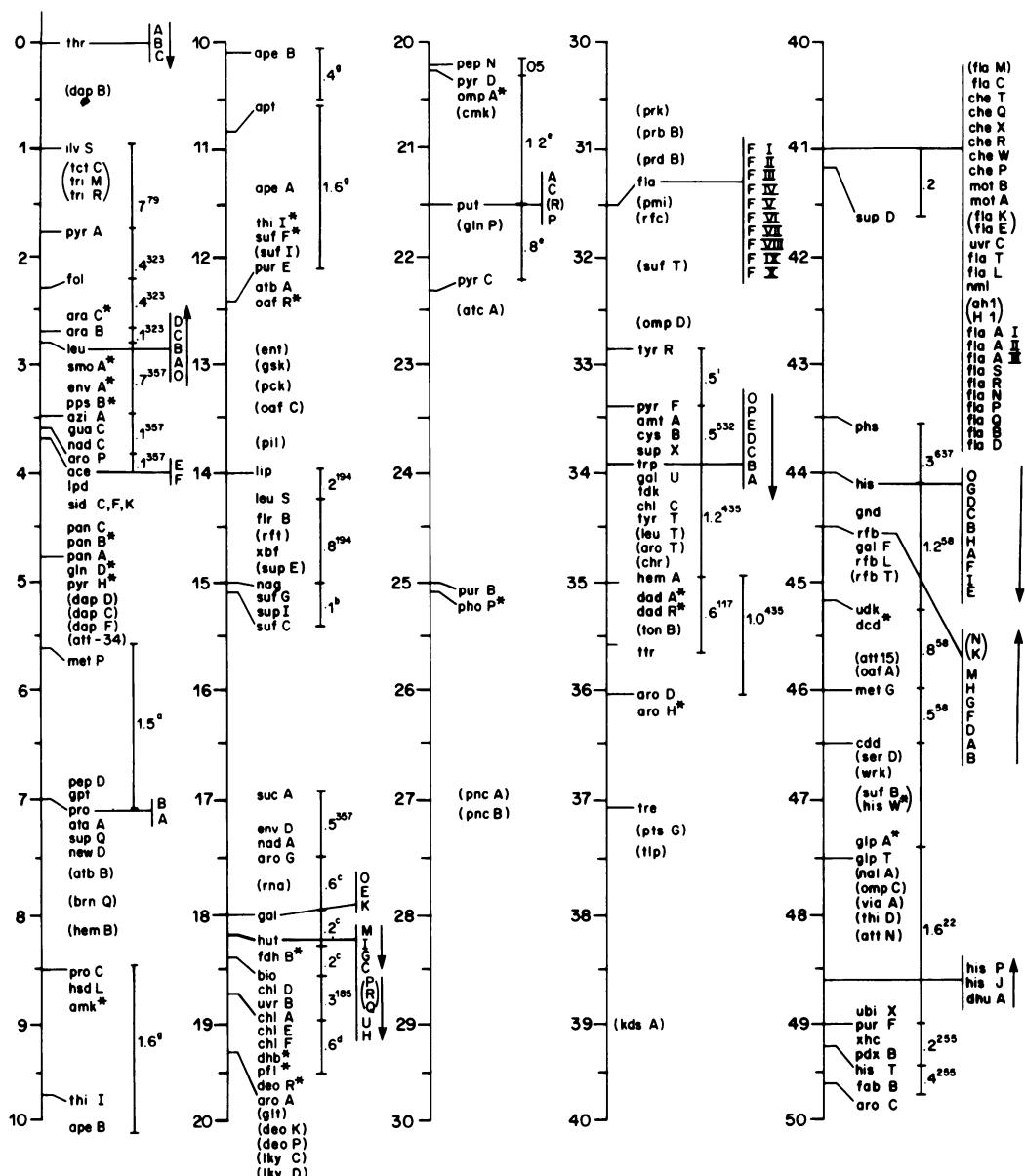


FIG. 2. Linkage map of *S. typhimurium*, represented as 10 segments. The scale of 100 U begins at zero for the *thr* loci, as in previous maps (526, 527, 529, 531) and in the linkage map of *E. coli* K-12 (46). The segmented line to the right of the gene symbols indicates that the genes are jointly transduced; the numbers to the right of the segmented line indicate the linear distance between genes. This linear distance was determined from the frequency of joint transduction and was calculated assuming that the length of P22, KB1, and ES18 transducing fragments is 1 U while that of P1 phage is 2 U and applying the formula developed by Kemper (323) to convert the percentage of joint transduction to map distance. The superscript to the number indicating the linear distance is the reference giving the data used for calculation; a number comes from Literature Cited, while a letter indicates a personal communication which is listed below. The genetic symbols are defined in Table 1. Parentheses around a gene symbol indicate that the location of the gene is known only approximately, usually from conjugation studies. An asterisk indicates that a marker has been mapped more precisely, usually by phage-mediated transduction, but that its position with respect to adjacent markers is not known. Arrows to the extreme right of genes and operons indicate the direction of messenger ribonucleic acid transcription by these loci. A line without an arrowhead to the extreme right of a gene or operon indicates that the orientation of the genes on the linkage map is not known. The following letters indicate superscripts to the length of the gene interval and show that the interval is based on a personal communication from the following persons: (a) T. Mojica-a and P. D. Ayling; (b) G. Roberts and J. R. Roth; (c) W. Brill; (d) M.-C. Pascal; (e) J. R. Roth; (f) J. Stephens; (g) C. G. Miller; (h) H. Kozdroj and T. Kłopotowski; (i) E. Gollub and D. B. Sprinson; and (k) J. Gots.

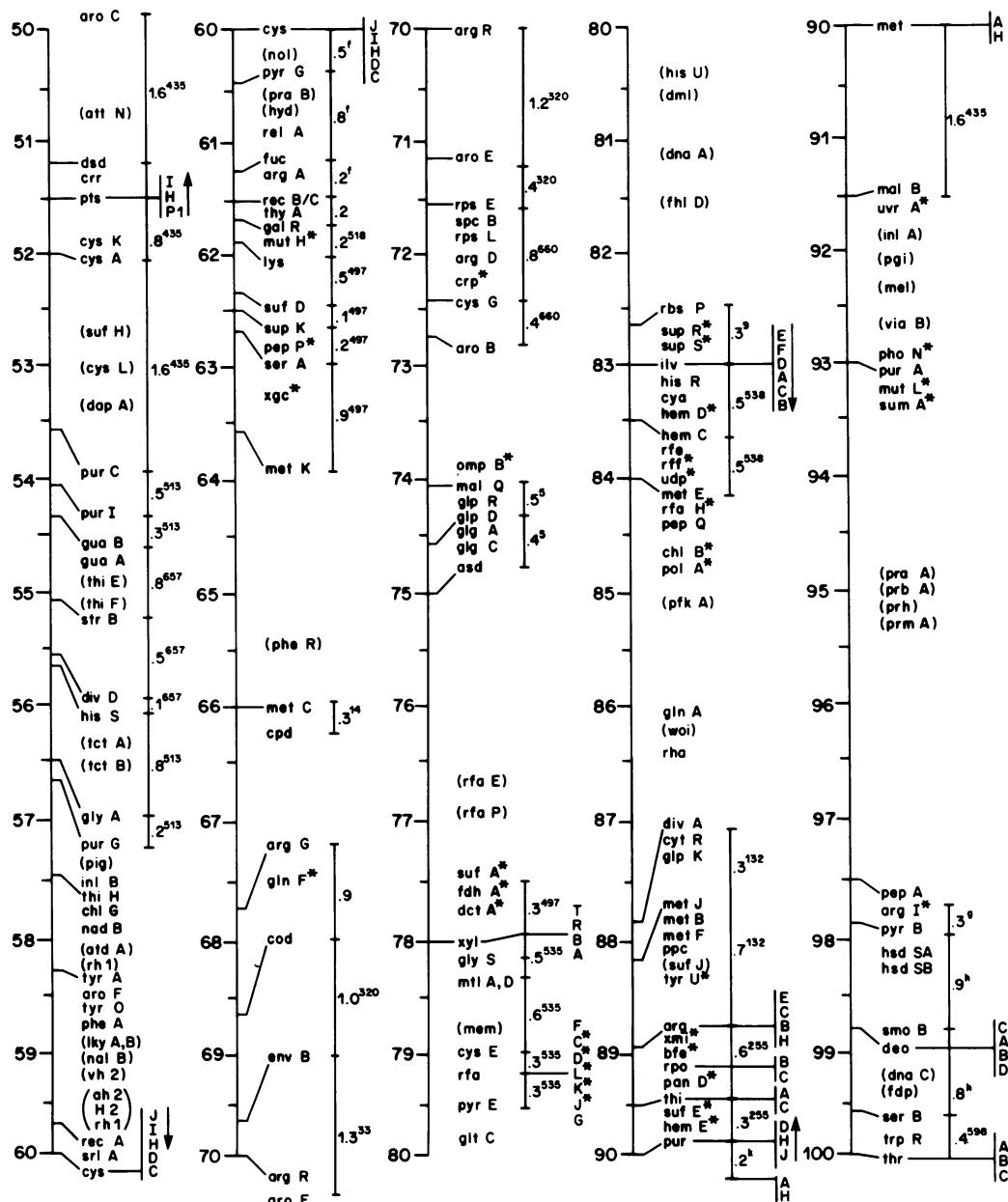


FIG. 2. *Right.*

gene in *E. coli* and *S. typhimurium* may result in sufficiently unlike phenotypes that recognition of their allelism may be difficult. A case in point is that of the genes *tonA* and *tonB*, recognized originally in *E. coli* as specifying sites for adsorption of phage T1 and subsequently found to be required for the adsorption of other phages and colicins and, in the case of *tonB*, for

adsorption of enterochelin. Recent data indicate that alleles of both genes exist in *S. typhimurium*, at comparable locations on the linkage map (221), but that the phenotypes determined by the alleles are not identical. The gene *sidK* appears to be homologous to *tonA* of *E. coli* (221, 387). Although *tonB* is responsible for enterochelin adsorption in both genera, in *E. coli*

TABLE 1. Genes of *S. typhimurium*

Genetic symbol	Mnemonic	Former or alternative symbol; enzyme deficiency or other phenotype <sup>a</sup>	Homologous gene in <i>E. coli</i> <sup>b</sup>	Map position (U) <sup>c</sup>	References <sup>d, e</sup>
<i>aceE</i>	Acetate	Acetate requirement; pyruvate dehydrogenase (pyruvate:cytochrome b <sub>1</sub> oxidoreductase; EC 1.2.2.2)	<i>aceE</i>	4	357
<i>aceF</i>	Acetate	Acetate requirement; pyruvate dehydrogenase (pyruvate:lipoate oxidoreductase; EC 1.2.4.1)	<i>aceF</i>	4	357
<i>ah1</i>		<i>Ah1A; Ah1C</i> ; activator of <i>H1</i>		41	187, 196, 273, 275
<i>ah2</i>		<i>Ah2</i> ; activator of <i>H2</i>		59	187, 185, 272, 274, 670b
<i>amk</i>		AMP kinase		9	J
<i>amtA</i>		Resistance to 40 mM 3-amino-1,2,4-triazole in presence of histidine		34	645
<i>apeA</i>		Endoprotease (hydrolyzes N-acetyl-L-phenylalanine-β-naphthyl ester)		11	428, 431
<i>apeB</i>		Endoprotease (hydrolyzes N-acetyl-L-phenylalanine-β-naphthyl ester)		10	R
<i>apt</i>		Endoprotease (hydrolyzes N-acetyl-L-phenylalanine-β-naphthyl ester)		11	R
<i>araA</i>	Arabinose	L-Arabinose isomerase (EC 5.3.1.4)	<i>araA</i>	NM	74
<i>araB</i>	Arabinose	Ribulokinase (EC 2.7.1.16)	<i>araB</i>	2	124
<i>araC</i>	Arabinose	Regulatory gene for arabinose catabolic enzymes	<i>araC</i>	2	75
<i>argA</i>	Arginine	<i>argB</i> ; amino acid acetyltransferase (EC 2.3.1.1)	<i>argA</i>	61	307
<i>argB</i>	Arginine	<i>argC</i> ; N-acetyl-γ-glutamokinase (EC 2.7.2.8)	<i>argB</i>	89	
<i>argC</i>	Arginine	<i>argH</i> ; N-acetyl-γ-glutamyl phosphate reductase (EC 1.2.1.38)	<i>argC</i>	89	
<i>argD</i>	Arginine	<i>argG</i> ; acetyltornithine aminotransferase (EC 2.6.1.11)	<i>argD</i>	72	69
<i>argE</i>	Arginine	<i>argA</i> ; acetyltornithine deacetylase (EC 3.5.1.16)	<i>argE</i>	89	
<i>argG</i>	Arginine	<i>argE</i> ; argininosuccinate synthetase (EC 6.3.4.5)	<i>argG</i>	68	
<i>argH</i>	Arginine	<i>argF</i> ; argininosuccinate lyase (EC 4.3.2.1)	<i>argH</i>	89	193, 194
<i>argI</i>	Arginine	Ornithine carbamoyltransferase (EC 2.1.3.3)	<i>argI</i>	98	4, 319, 321
<i>argP</i>	Arginine	Arginine transport	<i>argP</i>	NM	480
<i>argR</i>	Arginine	L-Arginine regulation	<i>argR</i>	70	320, 322
<i>argS</i>	Arginine	Arginyl-tRNA synthetase (EC 6.1.1.19)	<i>argS</i>	NM	467
<i>aroA</i>	Aromatic	3-Enolpyruvylshikimate 5-phosphate synthetase	<i>aroA</i>	19	
<i>aroB</i>	Aromatic	5-Dehydroquinate synthetase	<i>aroB</i>	73	
<i>aroC</i>	Aromatic	<i>aroD</i> ; chorismate synthetase	<i>aroC</i>	50	
<i>aroD</i>	Aromatic	<i>aroE</i> ; 5'-dehydroquinate dehydratase (EC 4.2.1.10)	<i>aroD</i>	36	
<i>aroE</i>	Aromatic	<i>aroC</i> ; 5-dehydroshikimate reductase	<i>aroE</i>	71	
<i>aroF</i>	Aromatic	Tyrosine-repressible DAHP synthetase	<i>aroF</i>	59	155, 156
<i>aroG</i>	Aromatic	Phenylalanine-repressible DAHP synthetase	<i>aroG</i>	17	
<i>aroH</i>	Aromatic	Tryptophan-repressible DAHP synthetase	<i>aroH</i>	36	265
<i>aroP</i>	Aromatic	Aromatic amino acid transport	<i>aroP</i>	3	52
<i>aroT</i>	Aromatic	Ability to transport tryptophan, phenylalanine, tyrosine		34	619
<i>asd</i>		Aspartate-semialdehyde dehydrogenase (EC 1.2.1.11)	<i>asd</i>	75	
<i>ataA</i>		<i>attP22</i> I; attachment site for prophage P22	<i>attP22</i>	7	257, 300, 301
<i>atbA</i>		<i>attP27</i> I; attachment site for prophage P27		12	

TABLE 1—Continued

Genetic symbol	Mnemonic	Former or alternative symbol; enzyme deficiency or other phenotype <sup>a</sup>	Homologous gene in <i>E. coli</i> <sup>b</sup>	Map position (U) <sup>c</sup>	References <sup>d, e</sup>
<i>atbB</i>		<i>attP27</i> II; Second attachment site for prophage P27		8	
<i>atcA</i>		<i>attP221</i> ; attachment site for prophage P221		23	668
<i>atdA</i>		<i>attP6</i> , <i>attP14</i> ; attachment site for prophage P6, or P14 in group C <i>Salmonella</i>		58	
<i>attN</i>		Attachment site for prophage N in <i>S. montevideo</i>		51	151
<i>att15</i>	Attachment	Attachment site of phage $\epsilon^{15}$ to chromosome of group E <i>Salmonella</i>		45	338, 420
<i>att34</i>	Attachment	Attachment site of phage $\epsilon^{34}$ to chromosome of group E <i>Salmonella</i>		5	339, 420
<i>aziA</i>	Azide	Resistant to 3 mM sodium azide on L-methionine	<i>azi</i>	3	132, 133
<i>bfe</i>	Biotin	Adsorption of phage BF23 and colicin E Requirement	<i>bfe</i>	89	228, 436
<i>bio</i>			<i>bioA</i>	18	
<i>brnQ</i>		<i>ilvT</i> ; branched-chain amino acid transport	<i>brnQ</i>	8	332, 334
<i>cdd</i>		Cytidine deaminase (EC 3.5.4.5)	<i>cdd</i>	46	293a, 321
<i>cheP</i>		Chemotaxis		40	41–43, 136, 149, 348, 349, 398–401a, 432, 583, 616, 617, 631a, 638
<i>cheQ</i>		Chemotaxis		40	41–43, 136, 149, 348, 349, 398–401a, 432, 583, 616, 617, 631a, 638
<i>cheR</i>		Chemotaxis; protein methylase		40	41–43, 136, 348, 349, 582, 583, 616, 617, 638
<i>cheS</i>		Chemotaxis		NM	43, 638
<i>cheT</i>		Chemotaxis		40	43, 617, 638
<i>cheW</i>		Chemotaxis		40	43, 638
<i>cheX</i>		Chemotaxis		40	43, 136, 638
<i>chlA</i>	Chlorate	Resistance; affects nitrate reductase, tetrahydronate reductase, chlorate reductase, and hydrogen lyase	<i>chlA</i>	19	185
<i>chlB</i>	Chlorate	Resistance; affects nitrate reductase, tetrahydronate reductase, and hydrogen lyase	<i>chlB</i>	84	116, 118
<i>chlC</i>	Chlorate	Resistance; affects nitrate reductase	<i>chlC</i>	34	115, 117
<i>chlD</i>	Chlorate	Resistance; affects nitrate reductase, tetrahydronate reductase, chlorate reductase, and hydrogen lyase	<i>chlD</i>	18	13, 185
<i>chlE</i>	Chlorate	Resistance		19	185
<i>chlF</i>	Chlorate	Resistance		19	185
<i>chlG</i>	Chlorate	Resistance; affects nitrate reductase, tetrahydronate reductase, chlorate reductase, and hydrogen lyase		57	
<i>chr</i>	Chromium	<i>car</i> ; chromium sensitivity (possibly homologous with <i>tonB</i> of <i>E. coli</i> )		34	221
<i>cmk</i>	Coenzyme A	Cytidylate kinase (EC 2.7.4.14)		21	60
<i>coaA</i>		Pantothenate kinase; coenzyme A synthesis		NM	F
<i>cod</i>		Cytosine deaminase (EC 3.5.4.1)		69	320
<i>cpd</i>		cAMP phosphodiesterase (EC 3.1.4.17)		66	14, 15, 520
<i>crp</i>		cAMP receptor protein	<i>crp</i>	72	15, 30, 256, 346, 486, 492
<i>crr</i>		Factor III for sugar transport by phosphotransferase IIB' ( <i>ptsG</i> ) system		51	140–142, 521, 522
<i>cya</i>	cAMP	Adenylate cyclase (EC 4.6.1.1)	<i>cya</i>	83	15, 346, 486, 519, 522a, 523

TABLE 1—Continued

Genetic symbol	Mnemonic	Former or alternative symbol; enzyme deficiency or other phenotype <sup>a</sup>	Homologous gene in <i>E. coli</i> <sup>b</sup>	Map position (U) <sup>c</sup>	References <sup>d, e</sup>
<i>cysA</i>	Cysteine	Sulfate-thiosulfate transport (chromate resistance)	<i>cysA</i>	52	482
<i>cysB</i>	Cysteine	Cysteine regulation; positive control of L-cystine transport	<i>cysB</i>	34	54, 84, 126, 482
<i>cysC</i>	Cysteine	Adenylylsulfate kinase (EC 2.7.1.25)	<i>cysC</i>	60	160, 307, 482
<i>cysD</i>	Cysteine	Sulfate adenyltransferase (EC 2.7.7.4)	<i>cysD</i>	60	160, 307, 482
<i>cysE</i>	Cysteine	Serine acetyltransferase (EC 2.3.1.30)	<i>cysE</i>	79	61, 266
<i>cysG</i>	Cysteine	Seroheme component of sulfite reductase	<i>cysG</i>	73	
<i>cysH</i>	Cysteine	Adenylylsulfate reductase (EC 1.8.99.2)	<i>cysH</i>	60	160, 383
<i>cysI</i>	Cysteine	Heme protein component of sulfite reductase	<i>cysI</i>	60	160, 383
<i>cysJ</i>	Cysteine	Flavoprotein component of sulfite reductase	<i>cysJ</i>	60	160, 383, 384
<i>cysK</i>	Cysteine	<i>aziB</i> , <i>trzA</i> ; cysteine synthase (resistance to 1,2,4-triazole) (EC 4.2.99.8)		52	138, 266–268, 351
<i>cysL</i>	Cysteine	Resistance to selenate		53	267
<i>cytR</i>		Regulatory gene for <i>deo</i> operon and <i>udp</i> and <i>cdd</i> genes	<i>cytR</i>	88	
<i>dadA</i>		<i>dad</i> ; D-amino acid dehydrogenase (EC 1.4.99.1) (D-histidine, D-methionine utilization)		35	435, 650, 651
<i>dadR</i>		Insensitivity of <i>dadA</i> to catabolite repression	<i>dadR</i>	35	650
<i>dapA</i>	Diaminopimelate	Dihydropicolinate synthase (EC 4.2.1.52)	<i>dapA</i>	53	V
<i>dapB</i>	Diaminopimelate	Dihydropicolinate reductase	<i>dapB</i>	1	V
<i>dapC</i>	Diaminopimelate	Tetrahydropicolinate succinylase	<i>dapC</i>	5	V
<i>dapD</i>	Diaminopimelate	Succinyl-diaminopimelate aminotransferase (EC 2.6.1.17)	<i>dapD</i>	5	V
<i>dapF</i>	Diaminopimelate	Diaminopimelate epimerase (EC 5.1.1.7)		5	V
<i>dcd</i>		dCTP deaminase (EC 3.5.4.13)		45	58, 59
<i>dctA</i>		Transport of dicarboxylic acids	<i>dctA</i>	78	465, 595
<i>deg</i>	Degradation	Degradation of aberrant proteins		NM	122; R
<i>deoA</i>	Deoxyribose	<i>tpp</i> ; thymidine phosphorylase (EC 2.4.2.4)	<i>deoA</i>	99	77, 251, 295, 505
<i>deoB</i>	Deoxyribose	<i>drm</i> ; phosphopentomutase (EC 2.7.5.6)	<i>deoB</i>	99	251, 295, 505
<i>deoC</i>	Deoxyribose	<i>dra</i> ; phosphodeoxyribaldolase (EC 4.1.2.4)	<i>deoC</i>	99	143, 249, 252, 295–297, 505
<i>deoD</i>	Deoxyribose	<i>pnu</i> ; <i>pup</i> ; purine nucleoside phosphorylase (EC 2.4.2.1)	<i>deoD</i>	99	295, 504, 505
<i>deoK</i>	Deoxyribose	Deoxyribokinase		20	250, 541
<i>deoP</i>	Deoxyribose	Deoxyribose transport		20	250
<i>deoR</i>	Deoxyribose	Constitutive for enzymes of <i>deoA</i> , <i>B</i> , <i>C</i> , and <i>D</i>	<i>deoR</i>	20	76, 201
<i>dhuA</i>	D-Histidine	Utilization; increased activity of histidine-binding protein J		49	19–21, 354, 435
<i>divA</i>	Division	<i>wrkA</i> ; septum initiation defect		87	132, 133
<i>divD</i>	Division	Round-cell morphology		56	658
<i>dml</i>	D-Malate	Utilization		80	
<i>dnaA</i>	DNA	DNA initiation	<i>dnaA</i>	82	49–51
<i>dnaC</i>	DNA	DNA synthesis initiation and cell division uncoupling	<i>dnaC</i>	99	7, 8, 507, 557, 558, 578, 579
<i>dsd</i>		D-Serine dehydratase (D-serine sensitivity) (EC 4.2.1.14)	<i>dsd</i>	51	
<i>dum</i>		dUMP synthesis		NM	59

TABLE 1—Continued

Genetic symbol	Mnemonic	Former or alternative symbol; enzyme deficiency or other phenotype <sup>a</sup>	Homologous gene in <i>E. coli</i> <sup>b</sup>	Map position (U) <sup>c</sup>	References <sup>d, e</sup>
<i>eca</i>		Enterobacterial common antigen synthesis		NM	413, 631
<i>ent</i>	Enterochelin	<i>emb</i> , <i>asc</i> ; enterochelin (dihydroxybenzoylserine trimer)	<i>ent</i>	13	63, 366, 664
<i>envA</i>	Envelope	<i>divC</i> , <i>smaA</i> ; cell division defect; chain formation	<i>envA</i>	3	132
<i>envB</i>	Envelope	<i>bac</i> ; spherical cells; osmotic-sensitive defect	<i>envB</i>	70	
<i>envD</i>	Envelope	Autolysis; drug sensitivity; alterations in cell morphology		17	33
<i>fabB</i>	Fatty acid biosynthesis	$\beta$ -Ketoacyl acyl carrier protein synthetase I	<i>fabB</i>	49	255
<i>fdhA</i>		Formate hydrogenlyase complex; formate dehydrogenase		78	129, 130, 472
<i>fdhB</i>		Formate hydrogenlyase complex; formate dehydrogenase		18	130
<i>fdp</i>		Fructose-1,6-diphosphatase	<i>fdp</i>	99	
<i>fhlD</i>		Formate dehydrogenase 2 activity		81	130
<i>flaAI</i>	Flagella	Defect in flagellar synthesis		41	136, 258, 346, 564, 633, 661
<i>flaAII</i>	Flagella	<i>motC</i> , <i>cheV</i> ; defect in flagellar synthesis		41	136, 346, 633, 638
<i>flaAIII</i>	Flagella	Defect in flagellar synthesis		41	136, 346, 633, 661
<i>flaB</i>	Flagella	Defect in flagellar synthesis		41	136, 270, 346, 633, 661
<i>flaC</i>	Flagella	Defect in flagellar synthesis	<i>flaH</i>	41	136, 270, 346, 633, 661
<i>flaD</i>	Flagella	Defect in flagellar synthesis		41	136, 270, 346, 633, 661
<i>flaE</i>	Flagella	Defect in flagellar synthesis		41	136, 270, 346, 633, 661
<i>flaFI</i>	Flagella	Incomplete flagellar basal bodies		31	270, 607
<i>flaFII</i>	Flagella	Defect in flagellar synthesis		31	270, 607
<i>flaFIII</i>	Flagella	Defect in flagellar synthesis		31	270, 607
<i>flaFIV</i>	Flagella	Incomplete flagellar basal bodies		31	270, 607
<i>flaFV</i>	Flagella	No flagella, but basal bodies detected		31	270, 607
<i>flaFVI</i>	Flagella	Defect in flagellar synthesis		31	270, 607
<i>flaFVII</i>	Flagella	Defect in flagellar synthesis		31	270, 607
<i>flaFVIII</i>	Flagella	Incomplete flagellar basal bodies		31	270, 607
<i>flaFIX</i>	Flagella	Incomplete flagellar basal bodies		31	270, 607
<i>flaFX</i>	Flagella	Defect in flagellar synthesis		31	270, 607
<i>flaG</i>	Flagella	Defect in flagellar synthesis	<i>flaG</i>	NM	270
<i>flaK</i>	Flagella	Defect in flagellar synthesis		41	136, 270, 346, 633, 661
<i>flaL</i>	Flagella	No flagella, but hook-basal body complexes detected		41	136, 258, 270, 346, 347, 607, 633, 661
<i>flaM</i>	Flagella	Defect in flagellar synthesis	<i>flaG</i>	41	136, 270, 582, 661
<i>flaN</i>	Flagella	Defect in flagellar synthesis		41	136, 270, 661
<i>flaP</i>	Flagella	Defect in flagellar synthesis		41	270, 661
<i>flaQ</i>	Flagella	<i>cheU</i> ; defect in flagellar synthesis		41	270, 638, 661
<i>flaR</i>	Flagella	Superhooks, mostly without flagellin filament	<i>flaR</i>	41	346, 474, 660a
<i>flaS</i>	Flagella	Defect in flagellar synthesis		41	Z
<i>flaT</i>	Flagella	<i>cfs</i> ; defect in flagellar synthesis and/or suppressor of <i>cya</i> in flagellation		41	346
<i>flrB</i>	Fluoroleucine resistance	Leucine or isoleucine regulation, or both		14	10, 194
<i>fol</i>	Folate	Tetrahydrofolate dehydrogenase (folate reductase, trimethoprim resistance) (EC 1.5.1.3)	<i>folA</i>	2	323
<i>fuc</i>	Fucose	Fucose nonfermenting	<i>fuc</i>	61	W
<i>galC</i>	Galactose	Constitutive synthesis of specific galactose permease		NM	478
<i>galE</i>	Galactose	Hexose-1-phosphate uridylyltransferase (EC 2.7.7.12)	<i>galE</i>	18	459, 462, 652

TABLE 1—Continued

Genetic symbol	Mnemonic	Former or alternative symbol; enzyme deficiency or other phenotype <sup>a</sup>	Homologous gene in <i>E. coli</i> <sup>b</sup>	Map position (U) <sup>c</sup>	References <sup>d, e</sup>
<i>galF</i>	Galactose	<i>galE</i> ; modifier of UDP-glucose pyrophosphorylase		45	
<i>galK</i>	Galactose	Galactokinase (EC 2.7.1.6)	<i>galK</i>	18	13
<i>galO</i>	Galactose	Operator	<i>galO</i>	18	
<i>galP</i>	Galactose	Specific galactose permease		NM	477, 478, 632a
<i>galR</i>	Galactose	Regulation	<i>galR</i>	62	518
<i>galU</i>	Galactose	Glucose-1-phosphate uridylyltransferase (EC 2.7.7.9)	<i>galU</i>	34	186, 459
<i>gdh</i>		Glutamate dehydrogenase (EC 1.4.1.4)		88	460
<i>glgA</i>	Glycogen	Glycogen synthetase (EC 2.4.1.21)	<i>glgA</i>	75	589
<i>glgC</i>	Glycogen	Glucose-1-phosphate adenylyltransferase (EC 2.7.7.27)	<i>glgC</i>	75	589
<i>glnA</i>		Glutamine synthetase (EC 6.3.1.2)	<i>glnA</i>	86	73, 80, 94, 199, 356, 587, 622, 627, 628
<i>glnD</i>		Uridylyltransferase		5	202
<i>glnF</i>		Regulation of glutamine synthetase production		68	202
<i>glnP</i>		Glutamine transport (high-affinity system)		22	72, 73
<i>glpA</i>	Glycerol phosphate	Glycerol-3-phosphate dehydrogenase (anaerobic)	<i>glpA</i>	47	634, 634a
<i>glpD</i>	Glycerol phosphate	Glycerol-3-phosphate dehydrogenase (NAD <sup>+</sup> ) (EC 1.1.1.8)	<i>glpD</i>	75	5, 380, 634, 634a
<i>glpK</i>	Glycerol phosphate	Glycerol kinase (EC 2.7.1.30)	<i>glpK</i>	88	634, 634a; AA
<i>glpT</i>	Glycerol phosphate	<i>pgtA</i> ; sn-glycerol-3-phosphate transport	<i>glpT</i>	47	497, 522, 524, 634, 634a
<i>glpR</i>	Glycerol phosphate	Regulatory gene for <i>glpD</i> , <i>K</i> , and <i>T</i>	<i>glpR</i>	75	634, 634a
<i>glt</i>	Glutamate	Requirement	<i>glt</i>	20	
<i>gltC</i>	Glutamate	Growth on glutamate as sole source of carbon		80	B
<i>glyA</i>	Glycine	Serine hydroxymethyltransferase (EC 2.1.2.1)	<i>glyA</i>	57	584-586a
<i>glyS</i>	Glycine	Glycyl-tRNA synthetase (EC 6.1.1.14)	<i>glyS</i>	78	595, 596
<i>gnd</i>		Phosphogluconate dehydrogenase (EC 1.1.1.43)	<i>gnd</i>	44	456, 656
<i>gpd</i>		Glucosamine-6-phosphate deaminase		NM	523
<i>gpsA</i>		sn-Glycerol-3-phosphate dehydrogenase [NAD(P) <sup>+</sup> ] (EC 1.1.1.94)		NM	380
<i>gpt</i>		<i>gxu</i> ; guanine-hypoxanthine phosphoribosyltransferase (EC 2.4.2.8)		7	131, 217, 218
<i>gsk</i>		Guanosine kinase		13	302
<i>guaA</i>	Guanine	GMP synthetase (EC 6.3.4.1)	<i>guaA</i>	54	541
<i>guaB</i>	Guanine	IMP dehydrogenase (EC 1.2.1.14)	<i>guaB</i>	54	541
<i>guaC</i>		GMP reductase (EC 1.6.6.8)	<i>guaC</i>	3	65, 302; J
<i>H1</i>	H antigen	Phase-one flagellar antigen (flagellin)	<i>hag</i>	41	40, 111, 196, 258, 259, 270-274, 309-311, 314-316, 346, 401a, 453, 564, 605, 606, 661
<i>H2</i>	H antigen	Phase-two flagellar antigen (flagellin)	(None)	59	187, 196, 270-275, 564, 605, 606, 670b
<i>hemA</i>	Heme	δ-Aminolevulinate synthetase (EC 2.3.1.37)	<i>hemA</i>	35	435
<i>hemB</i>	Heme	Heme deficient	<i>hemB</i>	8	
<i>hemC</i>	Heme	Heme deficient; urogen I synthase	<i>hemC</i>	83	539
<i>hemD</i>	Heme	Heme deficient; uroporphyrinogen III cosynthase	<i>hemD</i>	83	538
<i>hemE</i>	Heme	Accumulates uroporphyrin III	<i>hemE</i>	89	164

TABLE 1—Continued

Genetic symbol	Mnemonic	Former or alternative symbol; enzyme deficiency or other phenotype <sup>a</sup>	Homologous gene in <i>E. coli</i> <sup>b</sup>	Map position (U) <sup>c</sup>	References <sup>d, e</sup>
<i>hisA</i>	Histidine	<i>N</i> -(5'-phospho-L-ribosylformimino)-5-amino-1-(5'-phosphoribosyl)-4-imidazolecarboxamide isomerase (EC 5.3.1.16)	<i>hisA</i>	44	97, 235, 285, 419, 485
<i>hisB</i>	Histidine	Imidazoleglycerolphosphate dehydratase (EC 4.2.1.19) plus histidinolphosphatase (EC 3.1.3.15) (bifunctional enzyme)	<i>hisB</i>	44	90, 91, 97, 235, 260-264, 419, 503
<i>hisC</i>	Histidine	Histidinol-phosphate aminotransferase (EC 2.6.1.9)	<i>hisC</i>	44	12, 97, 235, 239, 240, 288, 419, 501-503, 555, 670
<i>hisD</i>	Histidine	Histidinol dehydrogenase (EC 1.1.1.23)	<i>hisD</i>	44	12, 75a, 97, 105, 134, 235, 283, 288, 289, 419, 665, 669, 670
<i>hisE</i>	Histidine	Phosphoribosyl-ATP pyrophosphohydrolase	<i>hisE</i>	44	97, 235, 419
<i>hisF</i>	Histidine	Cyclase	<i>hisF</i>	44	97, 235, 419
<i>hisG</i>	Histidine	ATP phosphoribosyltransferase (EC 2.4.2.17)	<i>hisG</i>	44	62, 78, 93a, 125a, 135, 189, 211, 212, 235, 271, 342a, 342b, 350, 352, 419, 423, 424, 437a, 438, 438a, 468-470a, 550, 551, 575, 591a, 635, 637a, 648
<i>hisH</i>	Histidine	Amido transferase	<i>hisH</i>	44	97, 235, 419
<i>hisI</i>	Histidine	Phosphoribosyl-AMP cyclohydrolase (EC 3.5.4.19) (may be bifunctional with <i>hisE</i> )	<i>hisI</i>	44	97, 235, 419
<i>hisJ</i>	Histidine	Histidine-binding protein J for histidine permeation		49	19-23, 554, 655
<i>hisO</i>	Histidine	Operator-promoter	<i>hisO</i>	44	39, 97, 181-183, 212, 317, 513, 572, 591, 597, 656
<i>hisP</i>	Histidine	Permease		49	19-23, 52, 97, 240
<i>hisR</i>	Histidine	tRNA structural gene		83	97, 98, 565
<i>hisS</i>	Histidine	Histidyl-tRNA synthetase (EC 6.1.1.21)		56	97-99, 135, 157, 158, 167, 168, 367, 395, 513, 594, 657
<i>hisT</i>	Histidine	Pseudouridine modification of tRNA		49	97, 100, 104, 123, 144, 145, 154, 499, 513
<i>hisU</i>	Histidine	tRNA maturation		80	85, 86, 97, 513
<i>hisW</i>	Histidine	tRNA maturation		47	95, 97, 513
<i>hpt</i>		Hypoxanthine phosphoribosyl transferase (not EC 2.4.2.8, see <i>gpt</i> )		NM	64, 65, 217
<i>hsdL</i>	Host specificity	<i>hsplT</i> ; restriction-modification system	<i>hsd</i>	9	236, 237
<i>hsdSA</i>	Host specificity	<i>hsplS</i> ; restriction-modification system	<i>hsd</i>	98	137, 237, 569, 632
<i>hsdSB</i>	Host specificity	Restriction-modification system	<i>hsd</i>	98	107, 108, 137, 632
<i>hutC</i>	Histidine	Utilization; repressor		18	205, 229, 231, 232, 627, 628
<i>hutG</i>	Histidine	Formiminoglutamase (EC 3.5.3.8)		18	627, 628
<i>hutH</i>	Histidine	Histidine ammonia-lyase (EC 4.3.1.3)		18	230, 627, 628
<i>hutI</i>	Histidine	Imidazolonepropionase (EC 3.5.2.7)		18	627, 628
<i>hutM</i>	Histidine	Utilization; promoter for <i>hutIGC</i>		18	139, 205, 627, 628
<i>hutP</i>	Histidine	Utilization; promoter for <i>hutUH</i>		18	139, 205, 627, 628
<i>hutQ</i>	Histidine	Utilization; operator for <i>hutUH</i>		18	205, 627, 628
<i>hutR</i>	Histidine	Utilization; catabolite insensitivity of <i>hutUH</i>		18	627, 628
<i>hutU</i>	Histidine	Utilization; urocanate hydratase (EC 4.2.1.49)		18	627, 628
<i>hyd</i>		<i>fhlB</i> , <i>fhlC</i> ; hydrogenase		61	129, 130, 473
<i>ilvA</i>	Isoleucine	<i>ile</i> ; threonine dehydratase (EC 4.2.1.16)	<i>ilvA</i>	83	36, 110, 128, 153, 253a, 362, 372, 390, 581, 639, 640

TABLE 1—Continued

Genetic symbol	Mnemonic	Former or alternative symbol; enzyme deficiency or other phenotype <sup>a</sup>	Homologous gene in <i>E. coli</i> <sup>b</sup>	Map position (U) <sup>c</sup>	References <sup>d, e</sup>
<i>ilvB</i>	Isoleucine-valine	Acetolactate synthase (valine sensitivity) (EC 4.1.3.18)	<i>ilvB</i>	83	103, 209, 457, 458
<i>ilvC</i>	Isoleucine-valine	<i>ilvA</i> ; 2-acetolactate mutase (EC 5.4.99.3)	<i>ilvC</i>	83	38, 209, 254, 559, 560
<i>ilvD</i>	Isoleucine-valine	<i>ilvB</i> ; dihydroxyacid dehydratase (EC 4.2.1.9)	<i>ilvD</i>	83	38, 38a, 209
<i>ilvE</i>	Isoleucine-valine	<i>ilvC</i> ; branched-chain amino acid amino-transferase (EC 2.6.1.42)	<i>ilvE</i>	83	331, 333, 382, 581
<i>ilvG</i>	Isoleucine-valine	$\alpha$ -Acetoxyhydroxy acid synthetase (feedback inhibition insensitive)	<i>ilvG</i>	83	103, 457, 458
<i>ilvS</i>	Isoleucine	Isoleucyl-tRNA synthetase (EC 6.1.1.5)		1	79, 128
<i>inlA</i>	Inositol	Fermentation		92	601
<i>inlB</i>	Inositol	Fermentation		58	
<i>kat</i>	Catalase	<i>cls</i> ; catalase (EC 1.11.1.6)		NM	191
<i>kdsA</i>		Ketodeoxyoctonate synthesis		39	440a, 495–495c
<i>leuA</i>	Leucine	2-Isopropylmalate synthase (EC 4.1.3.12)	<i>leuA</i>	3	323, 360
<i>leuB</i>	Leucine	$\beta$ -Isopropylmalate dehydrogenase	<i>leuB</i>	3	
<i>leuC</i>	Leucine	$\alpha$ -Isopropylmalate isomerase subunit	<i>leuC</i>	3	324, 325
<i>leuD</i>	Leucine	$\alpha$ -Isopropylmalate isomerase subunit	<i>leuD</i>	3	324, 325
<i>leuO</i>	Leucine	Operator		3	93, 219, 481
<i>leuS</i>	Leucine	Leucyl-tRNA synthetase (EC 6.1.1.4)	<i>leuS</i>	14	
<i>leuT</i>	Leucine	Leucine transport		35	481, 619; E
<i>lev</i>		Levomycin resistance		NM	172
<i>lip</i>	Lipoic acid	Requirement	<i>lip</i>	14	
<i>lkyA</i>	Leaky	Leakage of periplasmic proteins		59	
<i>lkyB</i>	Leaky	Leakage of periplasmic proteins		59	
<i>lkyC</i>	Leaky	Leakage of periplasmic proteins		20	
<i>lkyD</i>	Leaky	Leakage of periplasmic proteins; morphology defect		20	642, 643
<i>lon</i>		Filamentous growth; radiation sensitivity; polyamine metabolism		NM	476
<i>lpd</i>		Lipoamide dehydrogenase (NADH) (EC 1.6.4.3)	<i>lpd</i>	4	357
<i>lys</i>	Lysine	Requirement	<i>lysA</i>	62	
<i>malB</i>	Maltose	Utilization	<i>malB</i>	91	
<i>malQ</i>	Maltose	Amylomaltase	<i>malQ</i>	74	5, 522, 523
<i>mel</i>	Melibiose	Utilization	<i>mel</i>	92	370, 522, 576
<i>mem</i>	Membrane	Sugar transport and membrane protein defective		79	478a
<i>metA</i>	Methionine	<i>metI</i> ; homoserine acetyltransferase (EC 2.3.1.31)	<i>metA</i>	90	510
<i>metB</i>	Methionine	Cystathione $\gamma$ -synthase (EC 4.2.99.9)	<i>metB</i>	88	
<i>metC</i>	Methionine	Cystathione $\gamma$ -lyase (EC 4.4.1.1)	<i>metC</i>	66	
<i>metE</i>	Methionine	Tetrahydropteroylglutamate methyltransferase (EC 2.1.1.14)	<i>metE</i>	84	539, 646
<i>metF</i>	Methionine	5,10-Methylenetetrahydrofolate reductase (EC 1.1.1.68)	<i>metF</i>	88	646
<i>metG</i>	Methionine	Methionyl-tRNA synthetase (EC 6.1.1.10)	<i>metG</i>	46	35, 224
<i>metH</i>	Methionine	$B_12$ -dependent homocysteine-N <sup>5</sup> -methyltetrahydrofolate transmethylase	<i>metH</i>	90	646, 647
<i>metJ</i>	Methionine	Methionine analog resistant	<i>metJ</i>	88	596, 647
<i>metK</i>	Methionine	S-adenosylmethionine synthetase activity (methionine analog resistant)	<i>metK</i>	64	42, 245–247, 540, 596
<i>metP</i>	Methionine	Methionine permease ( $\alpha$ -methyl methionine resistant)		6	45, 72
<i>mglB</i>	Methyl galactoside	Galactose-binding protein	<i>mglB</i>	NM	421, 478, 593, 655, 674, 675
<i>min</i>	Minicells	Cell division	<i>min</i>	NM	613

TABLE 1—Continued

Genetic symbol	Mnemonic	Former or alternative symbol; enzyme deficiency or other phenotype <sup>a</sup>	Homologous gene in <i>E. coli</i> <sup>b</sup>	Map position (U) <sup>c</sup>	References <sup>d,e</sup>
<i>motA</i>	Motility	Nonmotile, although flagellate	<i>mot</i>	41	270, 346, 661
<i>motB</i>	Motility	Nonmotile, although flagellate	<i>mot</i>	41	270, 346, 661
<i>mtLA</i>	Mannitol	D-Mannitol phosphotransferase enzyme IIA	<i>mtLA</i>	79	523
<i>mtlD</i>	Mannitol	Mannitol-1-phosphate dehydrogenase (EC 1.1.1.17)	<i>mtlD</i>	79	299
<i>mutG</i>	Mutator	Increases mutation in host chromosome, not in P22		NM	227
<i>mutH</i>	Mutator	Mutator	<i>mutH</i>	62	M
<i>mutL</i>	Mutator	Increases frequency of mutation	<i>mutL</i>	93	
<i>nadA</i>	Nicotinamide	<i>nicA</i> ; requirement	<i>nadA</i>	17	193a
<i>nadB</i>	Nicotinamide	<i>nicB</i> ; requirement	<i>nadB</i>	58	193a
<i>nadC</i>	Nicotinamide	Requirement	<i>nadC</i>	3	193a
<i>nag</i>		<i>N</i> -acetyl glucosamine non-utilization	<i>nag</i>	15	T
<i>nalA</i>	Nalidixic acid	Resistance or sensitivity, DNA gyrase	<i>nalA</i>	48	P
<i>nalB</i>	Nalidixic acid	Resistance or sensitivity	<i>nalB</i>	59	
<i>ndk</i>		Nucleosidediphosphate kinase (EC 2.7.4.6)		NM	207, 208
<i>newD</i>		Substitute gene for <i>leuD</i>		7	324, 325
<i>nit</i>	Nitrogen	Nitrogen metabolism		NM	102
<i>nml</i>	<i>N</i> -methyl-lysine	<i>N</i> -methyl-lysine in flagellar protein		41	347
<i>nol</i>		Norleucine resistance; possible defect in valine uptake or regulation		60	244
<i>oafA</i>	O antigen factor	<i>ofi</i> ; O-5; O-factor 5 (acetyl group)		46	337
<i>oafC</i>	O antigen factor	Determines factor 1 in group E <i>Salmonella</i>		13	339, 420
<i>oafR</i>	O antigen factor	Synthesis of O antigen 12 <sub>2</sub>		12	339, 411
<i>ompA</i>		Outer membrane protein 33K (= II* of <i>E. coli</i> )		20	63, 152, 313, 566; P
<i>ompB</i>		Outer membrane protein 36K (= Ib of <i>E. coli</i> )		74	63, 313, 566; P
<i>ompC</i>		Outer membrane protein 36K (= Ib of <i>E. coli</i> )		48	63, 313, 566; P
<i>ompD</i>		Outer membrane protein 34K		33	63, 313, 566; P
<i>opp</i>		Oligopeptide permease	<i>opp</i>	NM	16, 293
<i>panA</i>	Pantothenic acid	(?) to α-ketoisovaleric acid	<i>pan</i>	5	161
<i>panB</i>	Pantothenic acid	Ketopantoal dolase (EC 4.1.2.12)		5	161
<i>panC</i>	Pantothenic acid	Pantothenate synthetase (EC 6.3.2.1)		5	161
<i>panD</i>	Pantothenic acid	β-Alanine biosynthesis		89	461
<i>panT</i>	Pantothenate	Pantothenate transport		NM	F
<i>pck</i>		Phosphoenolpyruvate carboxykinase (ATP) (EC 4.1.1.49)		13	
<i>pdxB</i>		Pyridoxine requirement	<i>pdxB</i>	49	255
<i>pepA</i>		Peptidase A (similar to aminopeptidase I of <i>E. coli</i> )		97	427, 429, 431
<i>pepD</i>		<i>ptdD</i> ; <i>pepH</i> (carnosinase); peptidase D (a dipeptidase)		7	257, 335, 427, 429, 431
<i>pepN</i>		<i>ptdN</i> ; peptidase N (an amino peptidase, naphthylamidase)		20	427, 429, 431
<i>pepP</i>		<i>ptdP</i> ; peptidase P		63	293, 396, 431
<i>pepQ</i>		Peptidase Q		84	293, 396, 431
<i>pfkA</i>		6-Phosphofructokinase (EC 2.7.1.11)	<i>pfkA</i>	85	S
<i>pfl</i>		Pyruvate formate lyase		19	471
<i>pgi</i>		Glucosephosphate isomerase (EC 5.3.1.9)	<i>pgi</i>	92	
<i>pheA</i>		Chorismate mutase (EC 5.4.99.5)	<i>pheA</i>	58	

TABLE 1—Continued

Genetic symbol	Mnemonic	Former or alternative symbol; enzyme deficiency or other phenotype <sup>a</sup>	Homologous gene in <i>E. coli</i> <sup>b</sup>	Map position (U) <sup>c</sup>	References <sup>d,e</sup>
<i>pheR</i>	Phenylalanine	Regulator gene for <i>pheA</i>		65	213, 214
<i>phoN</i>		Nonspecific acid phosphatase		93	BB
<i>phoP</i>		Nonspecific acid phosphatase		25	BB
<i>phoS</i>		Periplasmic phosphate-binding protein		NM	544, 659
<i>phs</i>		Hydrogen sulfide production		43	636, 637
<i>pig</i>	Pigment	Brownish colonies		57	
<i>pil</i>		<i>fim</i> ; pili (fimbriae)	<i>pil</i>	14	150, 614
<i>pmi</i>	Mannose	Mannosephosphate isomerase (EC 5.3.1.8)		32	517, 592
<i>pmrA</i>		Polymixin resistance		95	385
<i>pncA</i>	Pyridine nucleotide cycle	Nicotinamide to nicotinic acid + NH <sub>3</sub>	<i>pncA</i>	27	I
<i>pncB</i>	Pyridine nucleotide cycle	Nicotinic acid + ATP + PRPP to nicotinic acid mononucleotide		27	I
<i>polA</i>	Polymerase	DNA nucleotidyltransferase (DNA polymerase I; EC 2.7.7.7)	<i>polA</i>	85	281, 282, 403, 404, 649, 670a
<i>pox</i>		Control of P22 lysogeny		NM	588, 620, 621
<i>ppc</i>		Phosphoenolpyruvate carboxylase (EC 4.1.1.31)	<i>ppc</i>	88	570
<i>ppsB</i>		Phosphoenolpyruvate synthase		3	110a
<i>praA</i>		Phage P221—receptor function		95	415, 450, 451
<i>praB</i>		Phage P221—receptor function		61	415, 450, 451
<i>prbA</i>		Phage ES18—receptor function		95	O
<i>prbB</i>		Phage ES18—receptor function		31	O
<i>prdB</i>		Phage PH51—receptor function		31	O
<i>prh</i>		Phage HK009—receptor function		95	O
<i>prk</i>		Phage HK068—receptor function		31	O
<i>proA</i>	Proline	Glutamate to glutamic- $\gamma$ -semialdehyde	<i>proA</i>	7	257, 300, 301, 434
<i>proB</i>	Proline	Glutamate to glutamic- $\gamma$ -semialdehyde	<i>proB</i>	7	257, 300, 301, 434
<i>proC</i>	Proline	Pyrrolidine-5-carboxylate reductase (EC 1.5.1.2)	<i>proC</i>	8	434
<i>proP</i>	Proline	Minor L-proline permease			Q
<i>psuA</i>		Suppressor of polarity		NM	D
<i>ptsF</i>	Phosphotransferase system	Fructose phosphotransferase enzyme IIA	<i>ptsF</i>	NM	523
<i>ptsG</i>	Phosphotransferase system	<i>glu</i> , <i>gpt</i> , <i>cat</i> ; glucose phosphotransferase enzyme IIB'-factor III (crr) system (methyl $\beta$ -D-glucoside)	<i>ptsG</i>	37	422, 477, 523; K
<i>ptsH</i>	Phosphotransferase system	<i>carB</i> ; phosphohistidine protein-hexose phosphotransferase (EC 2.7.1.69)	<i>ptsH</i>	51	140–142, 477, 522, 523
<i>ptsI</i>	Phosphotransferase system	<i>carA</i> ; enzyme I of the phosphotransferase system	<i>ptsI</i>	51	140–142, 477, 522, 523
<i>ptsM</i>	Phosphotransferase system	<i>man</i> , <i>mpt</i> ; mannose-glucose phosphotransferase enzyme IIA (2-deoxyglucose)	<i>ptsM</i>	NM	519, 523
<i>ptsP1</i>	Phosphotransferase system	Promoter for <i>ptsH,I</i>		51	140–142, 422
<i>purA</i>	Purine	Adenylosuccinate synthetase (EC 6.3.4.4)	<i>purA</i>	93	66, 531
<i>purB</i>	Purine	Adenylosuccinate lyase (EC 4.3.2.2)	<i>purB</i>	25	
<i>purC</i>	Purine	Phosphoribosylaminoimidazole-succinocarboxamide synthetase (EC 6.3.2.6)	<i>purC</i>	54	
<i>purD</i>	Purine	Phosphoribosylglycinamide synthetase (EC 6.3.4.13)	<i>purD</i>	90	
<i>purE</i>	Purine	Phosphoribosylaminoimidazole carboxylase (EC 4.1.1.21)	<i>purE</i>	12	302, 344a, 531
<i>purF</i>	Purine	Amidophosphoribosyltransferase (EC 2.4.2.14)	<i>purF</i>	49	201, 302, 344a

TABLE 1—Continued

Genetic symbol	Mnemonic	Former or alternative symbol; enzyme deficiency or other phenotype <sup>a</sup>	Homologous gene in <i>E. coli</i> <sup>b</sup>	Map position (U) <sup>c</sup>	References <sup>d, e</sup>
<i>purG</i>	Purine	Phosphoribosylformylglycinamide synthetase (EC 6.3.5.3)	<i>purG</i>	57	302
<i>purH</i>	Purine	Phosphoribosylaminoimidazolecarboxamide formyltransferase (EC 2.1.2.3)	<i>purH</i>	90	
<i>purI</i>	Purine	Phosphoribosylaminoimidazole synthetase (EC 6.3.3.1)	<i>purI</i>	54	
<i>purJ</i>	Purine	IMP cyclohydrolase (EC 3.5.4.10)		90	
<i>putA</i>	Proline	<i>putB</i> ; utilization; proline oxidase and pyrrolidine-5-carboxylate dehydrogenase; bifunctional enzyme (proline utilization)		21	162, 487, 488; Q
<i>putC</i>	Proline	Utilization; constitutive synthesis of <i>putA</i> and <i>putB</i> enzymes		21	162
<i>putP</i>	Proline	Utilization; major L-proline permease		21	Q
<i>putR</i>	Proline	Utilization; catabolite repression insensitivity of <i>putA</i> and <i>putB</i> enzymes		21	162
<i>pyrA</i>	Pyrimidine	<i>argD</i> ; <i>ars</i> ; <i>aus</i> ; carbamoyl-phosphate synthase (glutamine) (arginine + uracil requirement) (EC 2.7.2.9)	<i>car</i>	2	1, 2, 3, 124, 287, 323, 454
<i>pyrB</i>	Pyrimidine	Aspartate carbamoyltransferase (EC 2.1.3.2)	<i>pyrB</i>	98	192, 193, 319, 321, 454, 550, 609, 610, 653
<i>pyrC</i>	Pyrimidine	Dihydro-orotase (EC 3.5.2.3)	<i>pyrC</i>	22	321, 454, 550, 653
<i>pyrD</i>	Pyrimidine	Dihydro-orotate oxidase (EC 1.3.3.1)	<i>pyrD</i>	20	321, 454, 550, 653
<i>pyrE</i>	Pyrimidine	Orotate phosphoribosyltransferase (EC 2.4.2.10)	<i>pyrE</i>	79	321, 454, 550, 653
<i>pyrF</i>	Pyrimidine	Orotidine-5'-phosphate decarboxylase (EC 4.1.1.23)	<i>pyrF</i>	34	321, 435, 454, 550, 653
<i>pyrG</i>	Pyrimidine	Cytidine triphosphate synthetase (EC 6.3.4.2)	<i>pyrG</i>	60	294, 454
<i>pyrH</i>	Pyrimidine	Uridine monophosphate kinase	<i>pyrH</i>	5	312
<i>rbsP</i>	Ribose	Ribose-binding protein	<i>rbsP</i>	83	9, 593, 655
<i>recA</i>		Recombination deficient; degrades DNA	<i>recA</i>	60	179a, 180, 281, 397a, 402, 666, 670a
<i>recB/C</i>		Recombination deficient; exonuclease V		61	179a, 180, U
<i>relA</i>	RNA relaxed	RC; regulation of RNA synthesis	<i>relA</i>	61	39, 591, 656; W
<i>rfaC</i>	Rough	Lipopolysaccharide core defect; proximal heptose deficient	<i>rfa</i>	79	284, 533, 536
<i>rfaD</i>	Rough	D-Glycero-D-manno-heptose epimerase		79	365
<i>rfaE</i>	Rough	Lipopolysaccharide core defect; proximal heptose deficient		77	20, 24, 109, 204, 233, 238, 308, 389, 462, 571, 592
<i>rfaF</i>	Rough	Lipopolysaccharide core defect; distal heptose deficient		79	233, 238, 308, 389, 535, 592
<i>rfaG</i>	Rough	Lipopolysaccharide core defect; glucose I transferase		79	186, 308, 389, 440, 459, 517, 535, 592
<i>rfaH</i>	Rough	Lipopolysaccharide core defect; galactose I deficient		84	389, 592
<i>rfaJ</i>	Rough	Lipopolysaccharide core defect; glucose II transferase		79	389, 592
<i>rfaK</i>	Rough	Lipopolysaccharide core defect; glucose II deficient		79	308, 381, 389, 400, 592
<i>rfaL</i>	Rough	Lipopolysaccharide core defect; O-translocase		79	389, 592
<i>rfaP</i>	Rough	Lipopolysaccharide core defect; phosphorylation of heptose		77	308
<i>rfaA</i>	Rough	TDP-glucose pyrophosphorylase		44	109, 306, 327, 336-338, 389, 462, 592
<i>rfbB</i>	Rough	TDP-glucose oxidoreductase		44	389, 592
<i>rfbD</i>	Rough	TDP-rhamnose synthetase		44	340, 389, 592
<i>rfbF</i>	Rough	Glucose-1-phosphate cytidylyltransferase (EC 2.7.7.33)		44	389, 592

TABLE 1—Continued

Genetic symbol	Mnemonic	Former or alternative symbol; enzyme deficiency or other phenotype <sup>a</sup>	Homologous gene in <i>E. coli</i> <sup>b</sup>	Map position (U) <sup>c</sup>	References <sup>d, e</sup>
<i>rfbG</i>	Rough	CDP-glucose oxidoreductase		44	389, 592
<i>rfbH</i>	Rough	CDP-abequose synthetase		44	389, 592
<i>rfbK</i>	Rough	Phosphomannomutase ( <i>man-2</i> )		44	389, 592
<i>rfbL</i>	Rough	Phosphomannomutase B		45	389, 592
<i>rfbM</i>	Rough	Mannose-1-phosphate guanylyltransferase (EC 2.7.7.22)		44	
<i>rfbN</i>	Rough	Galactose-diphosphoglycosyl carrier lipid synthetase		44	516, 517
<i>rfbT</i>	Rough	O-translocase		45	389, 592
<i>rfc</i>	Rough	<i>rouC</i> ; O-repeat unit not polymerized		32	389, 592
<i>rfe</i>	Rough	Defect in side-chain synthesis in <i>S. minnesota</i> and <i>S. montivideo</i>		84	308, 412-414
<i>rff</i>	Rough	Block in synthesis of enterobacterial common antigen		84	169, 413, 416
<i>rft</i>	Rough	"Transient" T1 forms		15	71
<i>rha</i>	Rhamnose	Utilization	<i>rha</i>	86	531
<i>rh1</i>		Regulator gene for <i>H1</i>		58	196; Z
<i>rna</i>		<i>rnsA</i> ; ribonuclease I	<i>rna</i>	18	106, 641
<i>rnc</i>		Ribonuclease III	<i>rnc</i>	NM	602
<i>rpoB</i>		<i>rif</i> ; RNA polymerase, beta subunit		89	50, 196a, 667
<i>rpoC</i>		RNA polymerase, beta-prime subunit		89	196a, 667
<i>rpsE</i>	Ribosomal protein, small	<i>spcA</i> ; 30S ribosomal subunit protein S5		72	660
<i>rpsL</i>	Ribosomal protein, small	<i>strA</i> ; 30S ribosomal subunit protein S12		72	660
<i>rts</i>		Reduction of thiosulfate		45	586
<i>serA</i>	Serine	Phosphoglycerate dehydrogenase (EC 1.1.1.95)		63	
<i>serB</i>	Serine	Phosphoserine phosphatase (EC 3.1.3.3)		99	
<i>serD</i>	Serine	Requirement for pyridoxine plus L-serine or glycine		47	C
<i>sidC</i>		Siderochrome utilization; ferrichrome transport; albamycin resistance		4	387, 388
<i>sidF</i>		Siderochrome utilization, ferrichrome transport; albamycin resistance		4	387, 388
<i>sidK</i>		Siderochrome utilization; albamycin resistance; receptor of phage ES18 in <i>S. typhimurium</i> and of T5 in <i>S. paratyphi</i> B	<i>tonA</i>	4	221, 387, 388; N, P
<i>smoA</i>		Smooth-colony morphology in histidine-constitutive mutants		3	475
<i>smoB</i>		Smooth-colony morphology in histidine-constitutive mutants		99	CC
<i>spcB</i>	Spectinomycin	Resistance; nonribosomal		72	660
<i>srlA</i>	Sorbitol	<i>gut</i> ; sorbitol-glucitol phosphotransferase enzyme II A	<i>srl</i>	59	342, 523
<i>strB</i>	Streptomycin	Low-level resistance plus auxotrophy; nonribosomal		55	464, 657, 660
<i>strC</i>		Streptomycin resistance, not <i>strA</i> or <i>B</i>		NM	220
<i>sucA</i>	Succinate	<i>suc</i> , <i>lys</i> + <i>met</i> ; succinate requirement; $\alpha$ -ketoglutarate dehydrogenase (decarboxylase component)	<i>sucA</i>	17	357
<i>sufA</i>		Frameshift suppressor affecting proline tRNA and correcting +1 frameshifts at runs of C in the message		77	497, 498
<i>sufB</i>		Frameshift suppressor affecting proline tRNA and correcting +1 frameshifts at runs of C in the message		46	497, 498

TABLE 1—Continued

Genetic symbol	Mnemonic	Former or alternative symbol; enzyme deficiency or other phenotype <sup>a</sup>	Homologous gene in <i>E. coli</i> <sup>b</sup>	Map position (U) <sup>c</sup>	References <sup>d, e</sup>
<i>sufC</i>		Recessive suppressor of +1 frameshift mutations at runs of C in the message		15	497, 498
<i>sufD</i>		Frameshift suppressor affecting glycine tRNA and correcting +1 frameshift mutations at runs of G in the message		63	496–498
<i>sufE</i>		Frameshift suppressor correcting +1 frameshift mutations at runs of G in the message		89	497, 498
<i>sufF</i>		Recessive frameshift suppressor correcting +1 frameshift mutations at runs of G in the message		12	497, 498
<i>sufG</i>		Frameshift suppressor correcting +1 mutations at runs of A in the message		15	DD
<i>sufH</i>		Frameshift suppressor		52	DD
<i>sufI</i>		Frameshift suppressor		12	DD
<i>sufJ</i>		Frameshift suppressor		88	95; L
<i>sumA</i>		Suppressor of missense		93	H
<i>supC</i>	Suppressor	See <i>tyrT</i>			
<i>supD</i>		Amber suppressor; serine insertion	<i>supD</i>	41	188; Y
<i>supE</i>		<i>supY</i> ; amber suppressor; glutamine insertion	<i>supE</i>	15	A
<i>supF</i>	Suppressor	See <i>tyrT</i>			
<i>supG</i>		Ochre suppressor; lysine insertion	<i>supG</i>	NM	Y
<i>supH</i>		Amber suppressor; leucine (?) insertion		NM	216; X, Y
<i>supI</i>		Nonsense suppressor induced by ICR-191 and allelic to <i>supG</i>		15	T
<i>supK</i>		<i>supT</i> ; recessive UGA suppressor, also corrects some frameshift mutations		62	44, 490, 629
<i>supM</i>		See <i>tyrU</i>			
<i>supQ</i>		Suppressor of nonsense and deletion mutations of <i>leuD</i>		7	324, 325
<i>supR</i>		Amber suppressor; haploid lethal		83	430
<i>supS</i>		UGA suppressor; haploid lethal		83	430
<i>supX</i>		<i>su-leu-500</i> ; suppressor of <i>leu-500</i>		34	171, 219
<i>tctA</i>		<i>tctI</i> ; tricarboxylic acid transport		56	269, 277–280
<i>tctB</i>		<i>tctII</i> ; tricarboxylic acid transport		56	270, 277–280
<i>tctC</i>		<i>tctIII</i> ; tricarboxylic acid transport		1	279
<i>tdk</i>		Thymidine kinase (EC 2.7.1.75)	<i>tdk</i>	34	255
<i>thiA</i>	Thiamine	<i>thiA</i> ; thiamine or thiazole moiety	<i>thiA</i>	89	
<i>thiC</i>		<i>thiC</i> ; thiamine or pyrimidine moiety	<i>thiC</i>	89	
<i>thiD</i>		Thiamine requirement		48	J
<i>thiE</i>		Thiazole type		55	J
<i>thiF</i>		Thiazole type		55	J
<i>thiH</i>		<i>thiB</i> ; thiamine requirement		58	EE
<i>thiI</i>		<i>thiC</i> ; thiazole type		10	J
<i>thrA</i>		<i>thrC,D</i> ; aspartokinase I and homoserine dehydrogenase I	<i>thrA</i>	0	209, 298, 599
<i>thrB</i>		<i>thrA</i> ; homoserine kinase (EC 2.7.1.39)	<i>thrB</i>	0	209, 599
<i>thrC</i>		<i>thrB</i> ; homoserine phosphate-β-meta-phosphatase	<i>thrC</i>	0	209, 599
<i>thyA</i>	Thymine	Requirement	<i>thyA</i>	62	307
<i>tkt</i>		Transketolase	<i>tkt</i>	NM	177
<i>tlp</i>		Loss of protease II		37	R
<i>tonB</i>		Determines resistance to ES18; determines a salmonellocin; affects iron transport; regulates levels of some outer membrane proteins	<i>tonB</i>	35	63; P
<i>tre</i>	Trehalose	Utilization		37	
<i>triM</i>		Tricarballylic acid metabolism		1	279

TABLE 1—Continued

Genetic symbol	Mnemonic	Former or alternative symbol; enzyme deficiency or other phenotype <sup>a</sup>	Homologous gene in <i>E. coli</i> <sup>b</sup>	Map position (U) <sup>c</sup>	References <sup>d, e</sup>
<i>triR</i>		Tricarballylic acid transport		1	279
<i>trpA</i>	Tryptophan	<i>trpC</i> ; tryptophan synthetase, component α (EC 4.2.1.20)	<i>trpA</i>	34	146, 147, 163, 165
<i>trpB</i>	Tryptophan	<i>trpD</i> ; tryptophan synthetase, component β (EC 4.2.1.20)	<i>trpB</i>	34	147, 165, 612b
<i>trpC</i>	Tryptophan	<i>trpE</i> ; N-(5-phosphoribosyl)anthranilate isomerase and indole-3-glycerol phosphate synthase (EC 4.1.1.48)	<i>trpC</i>	34	53, 147, 222, 377, 493
<i>trpD</i>	Tryptophan	<i>trpB</i> ; anthranilate phosphoribosyltransferase (EC 2.4.2.18)	<i>trpD</i>	34	147, 170, 222, 225, 226, 358, 506, 600
<i>trpE</i>	Tryptophan	<i>trpA</i> ; anthranilate synthase (EC 4.1.3.27)	<i>trpE</i>	34	124, 147, 222, 223, 225, 226, 363, 375, 376, 491, 506, 599, 612, 665a
<i>trpO</i>	Tryptophan	Operator	<i>trpO</i>	34	34, 53, 363a
<i>trpP</i>	Tryptophan	Promoter	<i>trpP</i>	34	34, 53
<i>trpR</i>	Tryptophan	Resistance to 5-methyltryptophan; depression of tryptophan enzymes	<i>trpR</i>	100	53, 598
<i>ttr</i>		Tetrathionate reductase		36	116
<i>tyrA</i>	Tyrosine	Requirement	<i>tyrA</i>	58	
<i>tyrO</i>	Tyrosine	Operator for <i>aroF</i> and <i>tyrA</i>	<i>aroK</i>	58	215
<i>tyrR</i>	Tyrosine	Regulator gene for <i>aroF</i> and <i>tyrA</i>	<i>tyrA</i>	33	155, 214
<i>tyrT</i>	tRNA <sub>i</sub> <sup>Tyr</sup>	<i>supC</i> ; ochre suppressor; tyrosine tRNA I; <i>supE</i> ; amber suppressor	<i>tyrT</i>	35	Y
<i>tyrU</i>	tRNA <sub>i</sub> <sup>Tyr</sup>	<i>supM</i> ; ochre suppressor; tyrosine tRNA II	<i>tyrU</i>	88	A, X
<i>ubiX</i>		Growth stimulation by <i>p</i> -hydroxybenzoic acid		49	22
<i>udk</i>		Uridine kinase (EC 2.7.1.48)	<i>udk</i>	45	
<i>udp</i>		Uridine phosphorylase (EC 2.4.2.3)	<i>udp</i>	84	
<i>uhpA</i>		Utilization of hexose phosphate		NM	
<i>uhpT</i>		Hexosephosphate transport	<i>uhpT</i>	NM	178, 179, 495
<i>unc</i>	Uncoupling	Membrane-bound ( $Mg^{2+}$ - $Ca^{2+}$ ) ATPase	<i>unc</i>	NM	92, 318, 673
<i>upp</i>		Uracil phosphoribosyltransferase (EC 2.4.2.9)	<i>upp</i>	54	
<i>ush</i>		UDP-glucose hydrolase		NM	618
<i>uvrA</i>	UV	Repair of UV damage to DNA; UV endonuclease, component A	<i>uvrA</i>	92	31, 32
<i>uvrB</i>	UV	Repair of UV damage to DNA; UV endonuclease, component B	<i>uvrB</i>	19	32, 281, 282, 567
<i>uvrC</i>	UV	Repair of UV damage to DNA	<i>uvrC</i>	38	568; GG
<i>uvrD/E</i>	UV	Repair of UV damage to DNA		NM	654, 670a; G
<i>valS</i>		Valyl-tRNA synthetase (EC 6.1.1.9)	<i>valS</i>	NM	467
<i>vh2</i>		VH2; control of rate of phase variation		59	196, 270
<i>viaA</i>		ViA; Vi antigen		48	576
<i>viaB</i>		ViB; Vi antigen (in <i>S. typhosa</i> )		94	576
<i>woi</i>		Increased yield of <i>hisO1242</i> transductants by <i>hisW1824</i> recipients		86	
<i>xbf</i>		<i>xdd</i> ; temperature-sensitive lethal		15	T
<i>xgc</i>		Temperature-sensitive lethal		63	U
<i>xhc</i>		Temperature-sensitive mutant linked to <i>purF</i> and <i>hisT</i>		49	255
<i>xmi</i>		Temperature-sensitive mutant linked to <i>argA</i> and <i>rif</i>		89	255
<i>xylA</i>	D-Xylose	Xylose isomerase (EC 5.3.1.5)	<i>xyl</i>	78	535, 556
<i>xylB</i>	D-Xylose	Xylulokinase (EC 2.7.1.17)		78	556
<i>xylR</i>	D-Xylose	Regulation		78	556
<i>xylT</i>	D-Xylose	Transport		78	556

TABLE 1—Continued

<sup>a</sup> Abbreviations: AMP, adenosine 5'-monophosphate; DAHP, 3-deoxy-D-arabinoheptulosonic acid-7-phosphate; ATP, adenosine 5'-triphosphate; ATPase, adenosine triphosphatase; CDP, cytidine 5'-diphosphate; dGTP, deoxyguanosine 5'-triphosphate; dUMP, deoxyuridine 5'-monophosphate; GMP, guanosine monophosphate; IMP, inosine 5'-monophosphate; NAD, nicotinamide adenine dinucleotide; NADP, nicotinamide adenine dinucleotide phosphate; PRPP, 5-phosphoribosyl-1-pyrophosphate; RNA, ribonucleic acid; TDP, thymidine 5'-diphosphate; tRNA, transfer ribonucleic acid; UDP, uridine 5'-diphosphate; UV, ultraviolet light.

<sup>b</sup> The homologous gene in *E. coli* K-12 is described in reference 46.

<sup>c</sup> Map positions are shown in Fig. 2. NM, Not mapped.

<sup>d</sup> Many of the references cited in earlier reviews are not repeated here to conserve space; those genes for which no new references are cited are indicated "see reference 529," but, for many other genes as well, additional references are in that source.

<sup>e</sup> Numbers refer to the Literature Cited section; letters refer to personal communications from the following sources: (A) D. Berkowitz, J. Hushon, and B. N. Ames; (B) B. Bochner; (C) J. Brenchley; (D) F. Chumley and J. Roth; (E) L. Corwin; (F) D. Dunn and E. Snell; (G) A. Eisenstark; (H) C. Field and J. Roth; (J) J. Gots; (K) Z. Hartman and P. E. Hartman; (L) T. Kohno, L. Bossi, and J. Roth; (M) M. Levinthal and C. A. Gritzammer; (N) M. Luckey; (O) P. H. Mäkelä; (P) P. H. Mäkelä and B. A. D. Stocker; (Q) R. Menzel; (R) C. G. Miller; (S) M. Ortega; (T) G. Roberts and J. Roth; (U) J. Roth; (V) C. W. Shuster and J. Betts; (W) J. Stephens; (X) F. Winston; (Y) F. Winston, D. Botstein, and J. Miller; (Z) S. Yamaguchi; (AA) M. Saier; (BB) L. Kier; (CC) H. Kozdroj and T. Klopotowski; (DD) T. Kohno and J. Roth; (EE) A. H. Stouthamer; (FF) R. T. Vinopal; and (GG) B. A. D. Stocker.

the allele determines a protein for T1 adsorption, while in *S. typhimurium* the allele determines a similar but nonidentical protein which is required for phage ES18 adsorption (221).

#### MATERIALS AND METHODS FOR GENETIC STUDIES

A variety of genetic techniques directly applicable to *Salmonella* are succinctly reviewed elsewhere (371, 433, 511, 529). A method of temporary culture storage (suspension in 1% NaCl) (353) has been added to widely used established methods (511). A versatile culture medium has been introduced (446).

#### F-Mediated Conjugation

The F-factor of *E. coli* K-12 has been transmitted into *S. typhimurium* (672) and *S. abony* (410) and Hfr strains have been isolated (for a list and description, see reference 534). In addition, some F-prime factors carrying *Salmonella* genetic material have been reported (534); these Hfr and F-prime factor strains are available from the *Salmonella* Genetic Stock Centre, University of Calgary. F-prime factors carrying *S. typhimurium* genes have not yet been isolated for all regions of the map of *S. typhimurium*, so *S. typhimurium* strains carrying F-prime factors containing *E. coli* genes (Table 3) have been used in a variety of studies, including: (i) complementation tests for allelism and, consequently, hints concerning linkage map position; (ii) dominance studies (190, 497, 657); (iii) diagnosis of enzyme quaternary structure (374); (iv) gene dosage studies (142, 657); (v) introduction of suppressors with known modes of action (406, 430); (vi) description of *Salmonella* mutation type or of suppressor gene type (70, 188, 512; F.

Winston and D. Botstein, personal communication); (vii) construction of P22 specialized transducing phages (257, 319); and (viii) detection of map locations of *E. coli* genes via gene dosage (422a) or electrophoretic mobility (234a) of the gene product in *Salmonella*. Low-efficiency transfer of some *E. coli* F-prime factors into *S. typhimurium* is due mainly to several restriction (*hsd*) barriers (26, 107, 108, 137, 237, 455, 569, 632). The restriction can be lessened through admixture of a third, intermediate, *S. typhimurium* host defective in restriction (e.g., strain SB5404 *hisI404 hsd proC51 rpsL667* plated on media lacking histidine and proline [B. Ely, L. Kops, and P. E. Hartman, unpublished data] or the *hsdLT6 hsdS29* strains of Stocker [186, 459]). Generally, *E. coli* K-12 F-prime factors in *S. typhimurium* undergo relatively little crossing-over and can be maintained as heterogenotes in Rec<sup>+</sup> genetic backgrounds. If RecA<sup>-</sup> recipients are preferred, they can be constructed by P22-mediated transduction, using phage grown on strain TT521 (*srl-2::trT517 recA1 rpsL*) and selection for tetracycline resistance (see Tet<sup>r</sup> Insertions, below); roughly half of the tetracycline-resistant recombinants are RecA (P. Anderson, in reference 342). F-prime factors in *Salmonella* transfer to *E. coli* K-12 with little restriction and have been used for: (i) placement of well-characterized *S. typhimurium* regulatory and deletion mutations into specialized transducing phage or plasmids (572; B. Ely and P. E. Hartman, unpublished data; W. Barnes, personal communication), (ii) construction of *E. coli* K-12 derivatives with *Salmonella* lipopolysaccharide and P22 sensitivity (306), (iii) studies of reversion responses of various *Salmonella* mutations carried by F-prime factors in K-12 strains defective in recombination or DNA re-

pair (D. Savić, personal communication; P. E. Hartman, unpublished data), and (iv) isolation of F-prime factors carrying the chromosomal replication origin of *S. typhimurium* (303).

TABLE 2. Alternative gene symbols<sup>a</sup>

Alternative symbol	Symbols in Table 1	Alternative symbol	Symbol in Table 1
<i>argA</i>	<i>argE</i>	<i>ilvT</i>	<i>brnQ</i>
<i>argB</i>	<i>argA</i>	<i>lys + met</i>	<i>sucA</i>
<i>argC</i>	<i>argB</i>	<i>man</i>	<i>ptsM</i>
<i>argD</i>	<i>pyrA</i>	<i>metI</i>	<i>metA</i>
<i>argE</i>	<i>argG</i>	<i>motC</i>	<i>flaA II</i>
<i>argF</i>	<i>argH</i>	<i>mpt</i>	<i>ptsM</i>
<i>argG</i>	<i>argD</i>	<i>nicA</i>	<i>nadA</i>
<i>argH</i>	<i>argC</i>	<i>nicB</i>	<i>nadB</i>
<i>aroC</i>	<i>aroE</i>	<i>ofi</i>	<i>oafA</i>
<i>aroD</i>	<i>aroC</i>	<i>pepH</i>	<i>pepD</i>
<i>aroE</i>	<i>aroD</i>	<i>pgtA</i>	<i>glpT</i>
<i>ars</i>	<i>pyrA</i>	<i>pnu</i>	<i>deoD</i>
<i>asc</i>	<i>ent</i>	<i>ptdD</i>	<i>pepD</i>
<i>attP22 I</i>	<i>ataA</i>	<i>ptdN</i>	<i>pepN</i>
<i>attP27 I</i>	<i>atbA</i>	<i>ptdP</i>	<i>pepP</i>
<i>attP27</i>	<i>atbB</i>	<i>pup</i>	<i>deoD</i>
<i>attP22I</i>	<i>atcA</i>	<i>rif</i>	<i>rpoB</i>
<i>attP6<sub>1</sub></i>	<i>atdA</i>	<i>rnsA</i>	<i>rna</i>
<i>attP14</i>	<i>atdA</i>	<i>rouA</i>	<i>rfc</i>
<i>aus</i>	<i>pyrA</i>	<i>smoA</i>	<i>envA</i>
<i>aziB</i>	<i>cysK</i>	<i>spcA</i>	<i>rpsE</i>
<i>bac</i>	<i>envB</i>	<i>strA</i>	<i>rpsL</i>
<i>car</i>	<i>chr</i>	<i>su-leu-500</i>	<i>supX</i>
<i>carA</i>	<i>ptsI</i>	<i>supC,F</i>	<i>tyrT</i>
<i>carB</i>	<i>ptsH</i>	<i>supM</i>	<i>tyrU</i>
<i>cat</i>	<i>ptsG</i>	<i>supT</i>	<i>supK</i>
<i>cfs</i>	<i>flaT</i>	<i>supY</i>	<i>supE</i>
<i>che</i>	<i>flaC</i>	<i>supZ</i>	<i>tyrT</i>
<i>cheU</i>	<i>flaQ</i>	<i>tctI</i>	<i>tctA</i>
<i>cheV</i>	<i>flaA II</i>	<i>tctII</i>	<i>tctB</i>
<i>cls</i>	<i>kat</i>	<i>tctIII</i>	<i>tctC</i>
<i>divC</i>	<i>envA</i>	<i>thiA</i>	<i>thiC</i>
<i>dra</i>	<i>deoC</i>	<i>thiB</i>	<i>thiH</i>
<i>drm</i>	<i>deoB</i>	<i>thiC</i>	<i>thiI</i>
<i>enb</i>	<i>ent</i>	<i>thiG</i>	<i>thiA</i>
<i>fhlB</i>	<i>hyd</i>	<i>thra</i>	<i>thrB</i>
<i>fhlC</i>	<i>hyd</i>	<i>thrb</i>	<i>thrC</i>
<i>fim</i>	<i>pil</i>	<i>thrc</i>	<i>thrA</i>
<i>fpr</i>	<i>tyrO</i>	<i>thrd</i>	<i>thrA</i>
<i>glu</i>	<i>ptsG</i>	<i>tpp</i>	<i>deoA</i>
<i>gpt</i>	<i>ptsG</i>	<i>trpA</i>	<i>trpE</i>
<i>gut</i>	<i>srlA</i>	<i>trpB</i>	<i>trpD</i>
<i>gxu</i>	<i>gpt</i>	<i>trpC</i>	<i>trpA</i>
<i>hspLT</i>	<i>hsdL</i>	<i>trpD</i>	<i>trpB</i>
<i>hspS</i>	<i>hsdSA</i>	<i>trpE</i>	<i>trpC</i>
<i>ile</i>	<i>ilvA</i>	<i>trzA</i>	<i>cysK</i>
<i>ilvA</i>	<i>ilvB</i>	<i>viA,B</i>	<i>viA,B</i>
<i>ilvB</i>	<i>ilvC</i>	<i>wrkA</i>	<i>divA</i>
<i>ilvC</i>		<i>xdd</i>	<i>xbf</i>

<sup>a</sup> The alternative symbols have been used in past publications. It is recommended that their use be abandoned and that the equivalent symbols, listed and described in detail in Table 1, be used in the future.

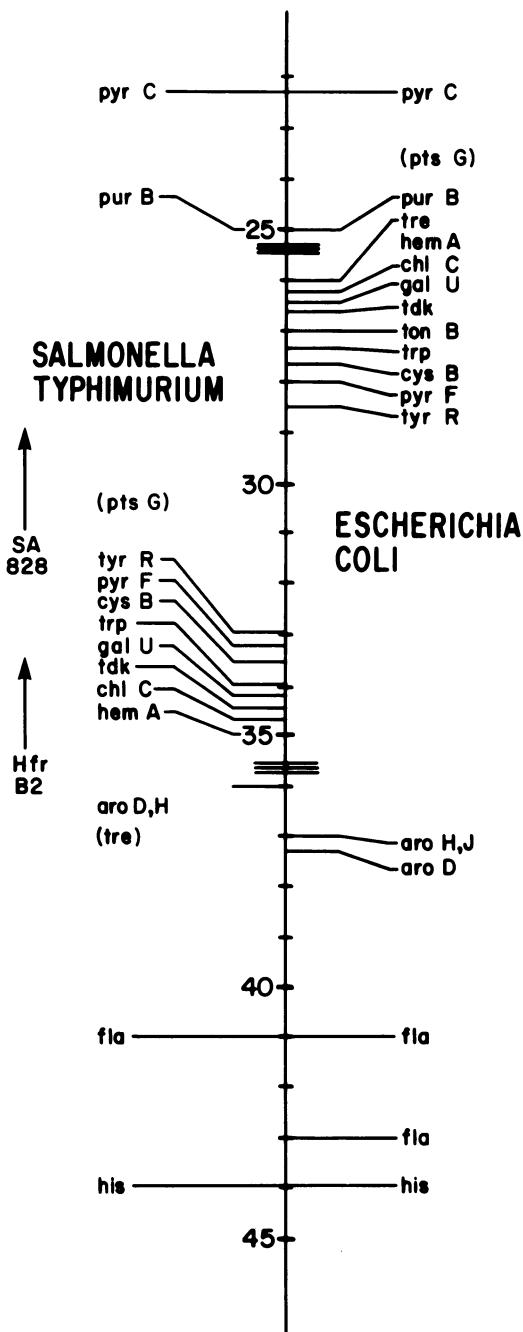


FIG. 3. Parts of the linkage maps of *E. coli* K-12 (redrawn from reference 46) and *S. typhimurium* (re-drawn from Fig. 2). The portion of the map from 25.5 to 35.5 U, inside the triple lines, is inverted between the two genera. Only those genes mapped in both genera are shown. The arrows at the left are the points of origin of two *Hfr* strains (534).

TABLE 3. Representative strains of *S. typhimurium* carrying defined F-prime factors originally derived from *E. coli* K-12

Approx min on <i>E. coli</i> map <sup>a</sup>	<i>E. coli</i> K-12 strain origin <sup>b</sup> (CGSC no.)	<i>Salmonella</i> strain <sup>c</sup>	Genotype ( <i>Salmonella</i> strain) <sup>d</sup>	Phenotype	Reference <sup>e</sup>	
1972 <sup>f</sup>	1976 <sup>g</sup>					
7-11	5.5-8	4288	TR2030	F'128/argI539 ΔproAB47	Arg <sup>-</sup>	257
10-?	7.8-7	Numerous		F' containing lacZ nonsense mutations	Lac <sup>-</sup>	70
10-14	7.8-11.7	5218	TR116	F'13/trp	Trp <sup>-</sup>	659
				F'13/purE66 pro-635	Pro <sup>-</sup>	497, 608
10-15	7.8-14.4	4282	SB5404	F'254/hisI404 proC51 rpsL667 hsd	His <sup>-</sup> Lac <sup>-</sup>	A
15-18	14-17.5	5104	TR125	F'100/aroP505 gal-501 hsdS10 ilvA405 proA46 purC7 rha-461 rpsL	Ilv <sup>-</sup> Pro <sup>-</sup> Pur <sup>-</sup>	B
15-18	14-17.5		SL4522	F'100 supL/leu-1051 hisC527 cysI1173 malB479	Leu <sup>-</sup> Cys <sup>-</sup> Sup ochre	406
21,21-30	21,21-32	4309		F'106, F'125/Δ-pyrD135	Pyr <sup>-</sup>	
32-34	37-37.5	4302	SB3220	F'148/hisI404 proC51 rpsL667 hsd	Pro <sup>-</sup>	A
35-40	40.5-44.5	4326	SB3198	F'150/hisD3052 Δchl <sup>r</sup> uvrB bio	Bio <sup>-</sup> , UV <sup>*</sup>	A
40-45	46-55	4210	SB3197	F'32/aroC5 cysC112	Cys <sup>-</sup>	A, C, D, E
			TR2145	F'32/aroC5 purF145 ilv-542	Ilv <sup>-</sup>	190, 497
45-46,	51.5-52,	4279	SB3073	F'142/guaA1 his-3217	His <sup>-</sup>	142, 657, 658
48-49	54-56.5					
49-55	56-61	4291	SB3185	F'143/aroC5 cysC1111	Phe <sup>-</sup> Trp <sup>-</sup> Tyr <sup>-</sup>	A
53-60	59.5-64.5	4254	TA3323	F'116/hisC2194 hisO1242 serA821	His <sup>-</sup>	490; C, F
			TR1524	F'116/hisC3072 hisO1242 ilv-563 lys-554 serA790	His <sup>-</sup> Ilv <sup>-</sup>	497
55-68	59.5-68	4257	SB3186	F'122/ΔproAB47 argD459	Pro <sup>-</sup>	A
60-66.5	67.5-74.5	4248	TA3326	F'141/argE116 his-1014	His <sup>-</sup>	F
60-71	64-79.8	4289	SB3188	F'140/ΔproAB47 argD459	Pro <sup>-</sup>	A
~65	~73		TR381	F'his <sup>+</sup> /ΔhisE1640	His <sup>+</sup>	374
73-79	80.5-90.5	4258	TA2249, TA2841	F'111/arg 519 hisO2321	His <sup>-</sup>	D
74-79	83-87.7	1206	SB3184	F'14/metB36 purG302	Gua <sup>-</sup> Thi <sup>-</sup>	190, 430; C
			TR632	F'14sup-1144/hisG200 ilvE201 metE338 pur-847	Pur <sup>-</sup>	430
74.5-79	83-88	4265	TA3324	F'133/ilvE12 tyrA506	Tyr <sup>-</sup>	F
76-80	84.5-90.5	4261	TR1731	F'110/hisF3704 hisO1242 ilv-565 thi-502	His <sup>-</sup> Ilv <sup>-</sup>	497
80-85	90-94	4259	TR1604	F'118/pyrB92 thr-115 trp-294	Thr <sup>-</sup> Trp <sup>-</sup>	608
83-88	93-98	4255	TR1603	F'117/pyrB92 thr-115 trp-294	Thr <sup>-</sup> Trp <sup>-</sup>	608

<sup>a</sup> End points approximate only.<sup>b</sup> CGSC, *E. coli* Genetic Stock Center.<sup>c</sup> Representative strains often containing auxotrophic markers for maintenance of F' and selection against host strain in transfer experiments.<sup>d</sup> F' numbers follow *E. coli* nomenclature (386). The symbols before the slash indicate the F' factor carried by the strain; the symbols after the slash show chromosomal mutations of the strain.<sup>e</sup> (A) B. Ely, L. Kops, and P. E. Hartman, unpublished data. (B) J. R. Roth, personal communication. (C) Same F' available in additional *Salmonella* strains; consult references. (D) B. N. Ames, personal communication. (E) G. F.-L. Ames, personal communication. (F) L. Kier and B. N. Ames, personal communication.<sup>f</sup> Reference 615.<sup>g</sup> Reference 46.

### DNA Transfection and Transformation

*S. typhimurium* protoplasts (67a, 68, 286) and some rough strains (109, 553) have been infected with P22 phage DNA ("transfection"). A modified transformation procedure for introduction of plasmid DNA has been developed (361). Availability of a *recBC* mutation in *S. typhimurium* (J. R. Roth, personal communication) may allow enhanced infectivity of linear input DNA molecules. DNA from *S. typhi* has been used to transform *E. coli* K-12 (525). It should be noted that artificially recombinant *S. typhimurium* DNA, constructed in vitro with restriction enzyme or ligase technology, currently is classified as P2:EK1 under United States National Insti-

tutes of Health Guidelines (444, 444a), and other countries also have placed specifications on use of bacteria containing such biochemically recombinant DNA molecules. Proposed revised Guidelines suggest that plasmids containing *Salmonella* LT2 DNA may be harbored either in *E. coli* or in *Salmonella* LT2 without special containment, vector, or other restrictions provided that special exemption is made in the future (see Introduction in reference 445). Such a revision involving bacteria well known to exchange chromosomal DNA by natural physiological processes promises to facilitate development of fundamental knowledge pertaining to *Salmonella*.

### Phage-Mediated Transduction

**Transduction methods.** Techniques useful in transduction tests are reviewed elsewhere (184, 433, 511, 529). Methodology for detection of P1-sensitive *S. typhimurium* mutants and their use in transduction tests has been developed (186, 210, 435, 459). P22 mutants are available for detection of *Salmonella* nonsense (82, 373a) and frameshift (629) suppressor mutations. An additional generalized transducing phage, unrelated to, but apparently of a similar size to, P22, has been isolated (83, 397).

Although the genetics of P22 phage has been reviewed (368), several recent advances bear on transduction and deserve brief mention. P22 lysogens receive transduced DNA with lowered efficiency ("superinfection exclusion"), but single and double *sie* mutants are available (603, 604). P22 mutants with high transducing (HT) ability afford greatly increased resolution in transduction tests (545, 546, 548). Although care must be taken to avoid carryover of transducing particles and multiple infections, integration-defective HT mutant P22 phage probably constitutes the best vehicle available for routine generalized transduction tests in *Salmonella*.

Phage-free colonies may be detected within phage-infected strains; after transduction with Int<sup>-</sup> phages, phage-infected colonies are dark green on green indicator plates (121). Indicator plates in which the concentrations of dyes used are less toxic have been developed (81).

**Transduction mechanisms.** Since about 50% of the particles in HT lysates carry bacterial DNA, HT phage should be of assistance in defining transduction mechanisms. It appears that, upon P22 infection, bacterial chromosomal DNA replication ceases (368), except for a few chromosomal regions whose semiconservation replication is mediated by P22 genetic information (47, 175). Otherwise, bacterial DNA present at the time of infection is preserved (547, 549) and packaged directly into phage coats as intact, phage-length pieces (176, 549). Packaging of transducing DNA appears to be as postulated by Ozeki and Ikeda (463) and mimics normal P22 head assembly and encapsulation of concatameric P22 phage DNA (87, 114, 329, 330). Packaging of linear double-stranded DNA starts at one preferred site, and phage-length sections are pruned off sequentially and unidirectionally along with particle maturation (292a, 549, 624, 626, 640a). Nonrandom distribution of transducing particles with apparent preferential end points in the bacterial DNA (463) does not seem to be due to mere chance distribution of double-strand breaks (125, 548). Since packaging proficiency appears highest for bacterial gene regions

richer in adenine-thymine base pairs which most closely reflect the base composition of P22 DNA (514, 561; P. E. Hartman, unpublished data), the initial cut may occur in a nucleotide sequence most likely to occur in chromosome regions rich in adenine plus thymine. HT mutations appear to affect a deoxyribonuclease specified by P22 phage gene 3 (483), leading to earlier and more efficient incorporation of bacterial DNA (549). In addition, HT mutant phage particles contain randomly permuted P22 genomes (623) in contrast to wild-type P22, in which the ends of the mature DNA fall within a preferred chromosomal region constituting about 20% of the P22 genome (626). The combined results suggest that incorporation of the bacterial chromosome (or sections of a P22 concatameric molecule) normally involves preferred DNA starting points, limited sequential encapsulation, and "headfull" packaging. P1 phage utilizes similar mechanisms (48, 234).

After injection into recipient bacteria, transduced DNA undergoes one of two fates. The first is abortive transduction, whereby about 90% of the injected bacterial DNA molecules persist and are transcribed but fail to be replicated (for P22 phage see references 176 and 463). In transduction with P1 phage, the abortively transduced molecules are phage-length, un-nicked, closed circular molecules whose termini are joined by a protein linker (536a); a unique protein has been found associated with transducing particles (276). The second is complete transduction, whereby about 10% of the input DNA molecules interact with the recipient chromosome; about one-fifth of the duplex molecule becomes covalently associated with host DNA as a double-stranded insertion, while about four-fifths of the molecule is degraded and the nucleotides are randomly reincorporated (176, 536a). HT phage and other types of P22 phages such as low-frequency-transducing mutants (483, 546) and specialized transducing phages (257, 301, 319, 625) should facilitate detailed analyses of these processes.

**P22 infection.** During phage infection, a P22 base-plate endorhamnosidase releases oligosaccharides from the lipopolysaccharide (291, 292), the membrane phospholipid composition changes (344), and cellular transport is temporarily affected (326, 484, 612a). These effects on the cell surface may underlie transient perturbations in enzyme induction (119) and increased cell permeability (345) during P22 infection. Defects in lipopolysaccharide are known to affect cell permeability (17, 442, 447, 500a, 533). The periplasmic space occupies 20 to 40% of the total cell volume of *S. typhimurium* (591b).

### Adding Markers to a Strain

Table 4 summarizes methodology useful in selection of new markers when multiply marked strains are desired. The methods rely on nearly identical map location of essentially all mutations that elicit a particular phenotype or combination of phenotypes, and most methods allow ready placement of previously defined mutations at specific points on the linkage map. Additional procedures applicable to insertion of selective markers are summarized by Miller (p. 225, reference 433). The availability of Tet<sup>r</sup> insertion strains (see below) opens up a multitude of additional possibilities in strain construction.

### Tet<sup>r</sup> Insertions

A most powerful new tool in *Salmonella* genetics uses a 8.3-kilobase transposable element

containing inverted repeat IS3 insertion sequences separated by a gene for tetracycline resistance (89, 341, 342). Convenient vehicles have been developed whereby chromosomal insertions of the Tet<sup>r</sup> transposable element can be detected through mere selection for tetracycline resistance. Insertion is clearly not random but does occur at many different chromosomal locations of which over 100 have been sorted out so far. Insertion mutations result in complete loss of function encoded by the damaged gene and are absolutely polar, allowing delineation of operons and internal promoters. Insertions have been found in the following *S. typhimurium* genes as inferred through phenotypes produced and verified, in a limited number of cases, by genetic analyses: *ade*, *ala*, *arg*, near *crp*, near *cya*, between *gnd* and *his*, *gua*, *hisC*, *hisD*, *hisF*, *hisG*, *hisH*, *hisI*, *hisJ*, *hisP*, between *his* and

TABLE 4. Methods useful for insertion of additional mutations into *S. typhimurium* strains

Map position		Marker involved	Type of mutation	Method <sup>a</sup>	Reference
1972 <sup>b</sup> (min)	1978 <sup>c</sup> (U)				
3	2	Various	Polar deletion →	See "Tet <sup>r</sup> Insertions"	89, 341, 342
		Localized	Missense	Mutagenized transducing phage; temperature selection	255
		Localized Auxotrophs	Various	Nitrosoguanidine comutagenesis	226a, 454a
		Various	Various	Selection in nalidixic acid	644
		<i>fol</i>	Deletion	Mutation and penicillin selection	433, 511
	10			Transduction to aminopterin resistance, replica plating for <i>ara</i> , <i>leu</i> , and <i>pyrA</i>	323
		<i>gpt</i>	Deletion	Transduction to 8-azaguanine resistance; replica plating for <i>pro</i>	218
		31, 41		Selection for resistance to chi phage	250
		18		Resistance to 2-deoxygalactose; selection for resistance to phage Felix-O, test for phage C21 sensitivity	13, 17, 652
		<i>fla</i> or <i>mot</i>	Various	Chlorate resistant anaerobically, replica plating for <i>gal bio</i>	13, 17
33	18	<i>galK</i>	Various, including deletion	Resistance to hydrazino imidazole propionic acid	562
		<i>chl'</i>	Deletion	Resistance to azaserine	355
		<i>hisP</i>	Various	Fosfomycin resistance	15, 15a, 133, 141
		<i>hisP,J</i>	Various	Fosfomycin resistance, replica plating	133, 141
		<i>glpT</i>	Various	1,2,4-Triazole resistance	142, 267, 319
	75	<i>ptsI</i>	Various		
		<i>cysK</i> ( <i>trzA</i> )	Various, including deletion		
		<i>cyaA</i>	Deletion	Transduction with <i>cysA20</i> and selection for chromate resistance	141, 422
		<i>thyA</i>	Various	Selection for resistance to trimethoprim on defined medium supplemented with thymine	
		<i>strB</i>	?	Low-level streptomycin resistance, replica plating for <i>Nic</i> <sup>-</sup> <i>Thi</i> <sup>-</sup>	657
108	72	<i>rpsL</i> (= <i>strA</i> )	Missense	High-level streptomycin resistance	
		<i>rfa</i> , <i>rfa</i>	Various	Selection for resistance to phage Felix O or P22	652
	41, 89	<i>rfaC,D,E,F</i> (lipopolysaccharide-core defects)	Various	Selection for resistance to phage Felix O, replica plating for deoxycholate sensitivity	536

<sup>a</sup> Additional methods are summarized by Miller (p. 225, reference 433).

<sup>b</sup> Reference 529.

<sup>c</sup> See Fig. 1.

*phs*, *ilvA*, *leu*, *lys*, *met*, *phe*, *pro*, near *proP*, *pur*, near *put*, *pyr*, near *pyrB*, near *relA*, *ser*, *srl*, *thi*, *thr*, *trp*, and *tyr* (342, 448; B. N. Ames, personal communication), and also between *purF* and *ubiX* (22). Positions of Tet' insertions outside of, but linked to, an existing marker can be located by P22-mediated cotransduction of tetracycline resistance and the marker in question. The insertion sites map as point mutations. Since the mutations are 100% associated with Tet', the mutations and nearby loci can be cotransduced to other strains via selection for Tet', an attribute enormously useful in strain construction. Tet' insertion mutants revert with precise excision of the Tet' element at frequencies centering around  $10^{-7}$  to  $10^{-8}$ , returning the gene to its wild-type condition. About  $10^4$  times more frequently, however, loss of Tet' occurs through genetic changes confined within the element itself (85% of cases) or through deletion or inversion of varying lengths of DNA to one side or to the other side of the insertion point (15% of cases). Deletions also occur that retain Tet', and these can be transduced into other strains by selection for Tet'. Thus, batteries of new deletion mutations should become available. Insertion of Tet' into an F' lac<sup>r</sup> plasmid in two opposite orientations furnishes genetic homology and allows selection of Hfr strains (at 42°C on lactose medium) which transfer the chromosome in one of the two directions from a fixed starting point originating at a chosen chromosomal Tet' insertion (F. Chumley and R. Menzel, personal communication). This will allow construction of numerous new Hfr strains. Finally, a P22 mutant (*bpl*) has been obtained that carries only half of the Tet' element; this phage lysogenizes at Tet' insertions and produces specialized transducing phages after induction. These, and still other possible uses of Tet' insertions and vehicles for Tet' transmission, have been discussed by the originators (89, 341, 342).

#### FIELDS OF SPECIAL INTEREST

##### Tandem Duplications

*Salmonella* carrying extended tandem duplications of various chromosomal regions are present in the population at a frequency of 0.01 to 10% for a given linkage map region (28). The end points of such duplications are nonrandomly distributed along the chromosome (27-29, 373, 430, 595, 596). There may be two types of duplications, those due to the *rec* system and involving chromosome regions with some homology of base sequence, and a second class not requiring *recA*<sup>+</sup> function and possibly involving IS sequences (28, 179a, 583a). Transduction of even large duplications to recipient bacteria can be observed provided that a selected donor marker

and the duplication junction are cotransducible (27). For many duplication strains, duplication loss occurs at a high rate and is dependent upon *recA*-mediated general recombination (27, 28, 441, 595). Some mutagens increase the frequency of duplications (253, 583a, 595). The adaptive value in nature of this propensity for duplication of gene blocks and its implications for gene distribution along the chromosome in "haploid" *Salmonella* remain to be assessed. A related question is the possibility of genetic exchange between bacterial species of potentially similar gene blocks (cf. 134a, 489). Partial diploids constitute a major class of recombinants in inter-species crosses (304, 305, 437).

#### Cryptic Plasmids and Prophages

*S. typhimurium* LT2 carries a resident plasmid of  $60 \times 10^6$  daltons (574, 580). The plasmid is retained in a *dnaC* mutant that cannot maintain some other plasmids (507, 578) and exhibits its own exclusion pattern toward superinfecting plasmids (25, 508, 580). The LT2 cryptic plasmid is associated with the *Salmonella* nucleoid (417) and can suppress a *dnaA* block in chromosomal replication through chromosomal integration (49). The cryptic plasmid apparently can recombine with other plasmids (418, 456), and such cointegrates account for stabilized F' lac elements (407-409, 509).

*S. typhimurium* LT2 also carries, at unknown locations on the chromosome, genetic information for at least two B prophages, one of which has been cured in a LT2 subline (671) and a second, Fels-1, which remains resident (197). A cryptic phage(s) is able to form a variety of recombinants with phage P22 (see 67, 257, and 663; references in 197) as can phage λ (88, 203, 663a). Levine et al. (369) discuss factors possibly important in facilitating recombination between resident and superinfecting heteroimmune phages. *S. typhimurium* strain LT7 also carries several prophages (67).

#### *Salmonelleae* as Pathogens

*S. typhimurium* researchers are reminded that many smooth sublines of strain LT2 remain virulent for mice (241) and mildly infectious at high doses for humans (56). Particular laboratory LT2 strains are 1,000 times less virulent for mice than are *S. typhimurium* strains isolated independently from nature (391a). Many decades of combined experience free from such overt infections in our own laboratories, and in many other laboratories, involving many thousands of man-years, convinces us that simple, standard clinical microbiological procedures offer adequate protection to personnel. Care in the handling, pipetting, and disposal of all materials

is stressed, however, as a general safety precaution. The several cases we have heard of in which a laboratory worker had a mild case of diarrhea due to an LT2 infection was caused by the worker swallowing a large dose while pipetting a thick resuspended cell paste or sonically treating a thick suspension of bacteria in a confined laboratory space. The complete smooth-form lipopolysaccharide is a definite prerequisite of virulence (500), and therefore lipopolysaccharide-defective rough mutants are safer to use, especially for batch cultures; in addition, cell extracts often fractionate more readily. They are easily obtained by selection with virulent smooth-specific phages (652). Acker (6) has called attention to Federal standards involving interstate shipment of *Salmonella* in the United States (6, 443); other countries have similar regulations. *S. typhi*, *S. paratyphi* A, B, and C, and *S. cholera suis* cause more serious disease and are probably more infectious in humans and so should be handled accordingly.

Enterobacterial infection and immunization are complex multistep processes that will never be understood well without the use of carefully characterized bacterial mutants. *S. typhimurium* is a prototype probe in analyses of these processes, as shown by the following examples (also see reference 573). Bacteria containing pili (fimbriae) are more infectious than Pil<sup>-</sup> *Salmonella* (150, 173), although bacteria lacking flagella, pili, or a complete lipopolysaccharide complex can still associate with and invade the ileal mucosa of infected gnotobiotic mice (614). Through the use of mutants, the enterobacterial common antigen has been shown to contribute to virulence (413, 631). Chemotaxis has been implicated in bacterial association with the mucosa (11), although cultures of nonmotile variants have long been thought to be as virulent as motile strains (37). Penetration of the intestinal mucosa is correlated with invasion of HeLa cells in a model system, but not with lipopolysaccharide content or 50% lethal dose (206, 328). The lipopolysaccharide is a major virulence determinant (391, 500, 630). Its polysaccharide part protects the bacteria from host defense mechanisms such as phagocytosis, while the lipid A part is responsible for the varied toxic effects of endotoxin (200). Other studies relate various lipopolysaccharide constituents to immunizing activity (166, 543) and virulence (391). Possibilities of developing protective immunization against enteric bacteria, based on shared antigenic determinants of the lipopolysaccharide core, lipid A, or enterobacterial common antigen, are being explored (413, 439).

*Salmonella* mutants also may shed light on the adaptive mechanisms that allow species to

occupy particular ecological niches, sometimes in humans. For example, strains of the chicken/turkey pathogen *S. pullorum* require cysteine for growth (343). Besides a block in a sulfate permease (*cysA*) component, *S. pullorum* contains a thermolabile sulfite reductase (248). The body temperature of fowl is high, and in vivo *S. pullorum* presumably utilizes the unusually high concentration of cysteine available for synthesis of feather protein, whereas outside of the host sulfite serves as the major sulfur source. Thus, *S. pullorum* appears to be a specialized, host-dependent organism. The fact that sulfate and the toxic anion chromate share a common permease (466) suggests streamlined and rational methodology for bacterial detection, enhancing chances of complete elimination of *S. pullorum* (cf. 243).

Most auxotrophic mutations in *S. typhimurium* do not reduce the virulence for mice (and it is worth noting that *S. typhi*, a *Salmonella* with no natural host except humans, is typically a tryptophan auxotroph), but mutants blocked in purine synthesis (241) or chlorate-resistant mutants (577) have decreased virulence for mice. Motile *Salmonella* species, such as *S. typhimurium*, may have a free-living existence apart from animal hosts (127), and laboratory experiments may be able to supplement epidemiological observation in increasing our knowledge of bacterial ecology. For example, membrane transport processes and chemotaxis (348, 349, 421) are certain to be important factors affecting the distribution of enteric species in nature.

#### Detection of Mutagens/Carcinogens

A carefully chosen and modified set of safe, deep rough *S. typhimurium* mutant strains (the Ames strains) is being used in literally hundreds of laboratories for in vitro detection of environmental mutagens/carcinogens in the presence and the absence of liver microsomes (17, 18, 101, 393, 394, 479, 600a). The method is amenable to detection of mutagens in urine (174) and in vivo ("host-mediated assay," reference 364). Treatment of free phage, induction of P22 and P221 prophages, and enhancement of phage-prophage recombination also have been used in *S. typhimurium* to detect genetically active compounds and analyze their modes of action (197, 198, 563, 611, 662, 663).

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